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DEER FROM LATE MIOCENE TO PLEISTOCENE OF THE WESTERN PALEARCTIC: SYSTEMATICS, PHYLOGENY AND EVOLUTION

Abstract of the doctoral thesis in biological sciences

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CONTENT

CONCEPTUAL CHARACTERISTICS OF RESEARCH

Scientific novelty and originality of the work. The doctoral thesis focuses on a crucial issue: the origin of modern biodiversity in an important systematic group (Mammalia, Ruminantia, Cervidae), which includes various vulnerable and endangered species. This research addresses a fundamental question about the evolution of life and provides critical insights into this particular group of animals. The Cervidae family is one of the world's most diverse groups of modern herbivores, with significant economic (domestication, hunting, medicine) and theoretical importance. Unfortunately, several species and subspecies of deer are endangered, and climate change has made the fate of vulnerable species unpredictable. However, valuable information about the origin of current deer biodiversity, evolutionary responses to climate change, and the mechanism of deer species extinction in the geological past can be gleaned from the paleontological record.

The western Palearctic's paleontological record holds special interest as it provides evidence of the extraordinary diversity of deer in this biogeographic zone's past (Croitor, 2018). Despite more than two centuries of fossil deer research in Europe, problems related to systematics and diversity of fossil deer remain unresolved, and several taxonomic issues remain in dispute. Additionally, the phylogenetic relationships between fossil and modern deer species are still unclear. A biogeographic approach to the study allows us to track the evolution of deer species and their diversity in a well-delimited geographical area that was deeply influenced by climatic conditions during the emergence and evolution of the western Palearctic zone.

This dissertation represents the first comprehensive study of fossil deer based on paleontological material from nearly the entire area of the western Palearctic, comprising 23 paleontological collections from 12 countries. The study includes taxonomic and systematic analyses of 27 genera and 78 species and forms of fossil deer, with the author describing two genera, three species, and one subspecies. The research provides new data and interpretations that fill critical gaps in the taxonomy and systematics of fossil and modern deer. Additionally, it proposes a new phylogenetic and evolutionary model of the deer family that sheds light on their evolutionary history (Croitor, 2022).

The description of the research domain state and the identification of research problems. In recent decades, our understanding of the taxonomic diversity of fossil deer has significantly increased. Several scholars have made important contributions to the understanding of the evolution and phylogeny of fossil deer from the western Palearctic. Notably, Azzaroli (1947, 1953), Kahlke (1956, 1997), Czyżewska (1968), Kototkevich (1970), Heintz (1970), Vislobokova (1990), Lister (1987), Azanza (2000), Stefaniak (2015), and other students have collected a vast amount of data on cervid paleontological records from the western Palearctic.

Nonetheless, despite the great abundance and diversity of fossil forms, their evolutionary and systematic interpretations are rather contradictory, and their relationships with living species are still unclear and speculative. In most cases, the difficulties in cervid classification are caused by poor or inadequate original descriptions of deer species, imprecise and vague definitions of taxa, and superficial or missing descriptions of type specimens. The insufficient knowledge of cervid species is further complicated by numerous synonymies, taxonomic confusions, and poor definitions of genera. Another unavoidable challenge is the absence of methodologically uniform criteria applied in the taxonomy and systematics of modern and fossil cervids.

While the taxonomy and systematics of modern deer are based on the combination of antler and cranial morphology (Flerov, 1952), the taxonomy of fossil deer is mostly based on antler morphology (Azzaroli, 1952; Heintz, 1970), and this circumstance is one of the significant methodological constraints. Cervid antlers are highly diversified and have undoubtedly systematic value since they reflect the ethologic diversity of fossil cervid species and thus ensured genetic isolation between them. However, cervid antlers are characterized by ontogenetic, geographic, and individual variability, which led to the description of a large number of synonymous species names based on variable and often fragmentary antlers (Heintz, 1970; Croitor, 2018). The shape of antlers is influenced by multiple factors of different natures (ecophysiological, morphofunctional, biomechanical, environmental, social, etc.), which are still insufficiently known (Bubenik, 1990).

Moreover, the incomplete and neglected record of the cranial morphology of fossil deer is another constraint for cervid taxonomy at the genus level (Vislobokova, 1990).

The objective of the dissertation is to explore the taxonomy, systematics, phylogeny, evolution, and paleobiogeography of fossil deer in the western Palaearctic from the Late Miocene to the end of the Pleistocene. The present study aims to achieve this objective through a thorough revision of the original type material and verification of all taxonomic acts that form the basis of the currently accepted views on the systematics of the family Cervidae.

Tasks of the dissertation: 1) conduct a taxonomic study by revising the type material, 2) verify the diagnoses of species and genera, 3) analyze the individual and evolutionary variability of cervids, 4) study the phylogenetic relationships of cervids, 5) identify the evolutionary mechanisms of cervids, and 6) reveal paleobiogeographic scenarios that explain the diversity of fossil cervids in the western Palearctic in the past.

Research hypothesis. Both subfamilies Cervinae and Capreolinae went through the holometacarpal stage of limbs, with different types of reduction of lateral metacarpals. The evolutionary radiation of Capreolinae occurred in western Eurasia during the Late Miocene. Plesiometacarpal deer dispersed for the first time into western Eurasia during the Early Pliocene after the mass extinction of telemetacarpal deer, which were represented in the Plio-Pleistocene record by only a few surviving lineages. The systematic gap between fossil and modern deer is artificial and can be bridged if the same taxonomic criteria are applied to both modern and fossil deer.

Research methodology. Special attention is given to the well-preserved fossil cranial material as it provides essential diagnostic characters and systematic information at the genus level (Vislobokova, 1990). Both morphological characteristics (selected anatomical parts' condition) and biometrical data are collected, and the taxonomical value of diagnostic characters is adjusted using molecular phylogeny data. To assess the taxonomic and systematic value of the morphological characters used in modern cervid systematics, a hierarchical cluster analysis of diagnostic craniodental characters (including antlers) was conducted. The hierarchical clustering paired group algorithm UPGMA was computed using the Jaccard Similarity Index for presence-absence data (PAST-4 application: Hammer et al., 2001). This approach helps to reveal the systematic position of fossil deer among modern representatives of the Cervidae family.

Scientific novelty and originality: the thesis proposes the first comprehensive taxonomic revision of fossil deer from Late Miocene to Late Pleistocene from western Palearctic zone based on the direct study of fossil material from the almost entire area of the western Palearctic (23 paleontological collections from 12 countries). Two genera, three species, and one subspecies described by the author. The study proposes the new phylogenetic model of crown deer (subfamilies Cervinae and Capreolinae) that reveals the phylogenetic relationships of fossil deer with previously uncertain phylogenetic position. The study for the first time applied evaluation of taxonomic significance of craniodental characters in cervids using the molecular genetic data and applied the obtained data in supervised hierarchical clustering in order to find the systematic position of fossil species among modern cervids.

The important scientific problem solved. The thesis presents a systematic and taxonomic revision of fossil deer from the western Palearctic, and proposes a new phylogenetic model for the crown cervids (subfamilies Cervinae and Capreolinae). For a long time, the origin of telemetacarpal deer (subfamily Capreolinae) remained obscure. Some authors hypothesized that the subfamily Capreolinae was related to North American Dremotheriinae, in an attempt to explain the missing paleontological record of the early evolutionary radiation of the telemetacarpal deer in Eurasia (Vislobokova, 1990). However, the study reveals the early stages of evolution of the subfamily Capreolinae in Europe during the Late Miocene, and clarifies the systematical position of poorly understood Late Miocene holometacarpal deer from southeastern Europe. Additionally, the systematical position of most fossil crown deer, including insular and North African endemics, is clarified.

Fundamentally new results for science and practice obtained. The thesis presents a new systematic and phylogenetic model for Eurasian crown cervids (subfamilies Cervinae and Capreolinae). By studying cervid systematic morphology, the phylogenetic relationships between mainland deer forms and their endemic insular Mediterranean relatives were revealed. As a result, two new cervid genera were established: *Haploidoceros* Croitor, Bonifay, and Brugal, 2008 from the Late Pleistocene of Western Europe, and *Praemuntiacus* Croitor, Zakharov, and Mararescul, 2020 from the Pliocene of Eastern Europe and China. Through the revision of fossil material, several new species and subspecies were also described, including *Praeelaphus australorientalis* Croitor, 2017 (from the Pliocene of Ukraine, Moldova, and Romania); *Rucervus gigans* Croitor, 2018 (from the Early Pleistocene of Greece); *Rucervus radulescui* Croitor, 2018 (from the Early Pleistocene of Romania); and *Cervus canadensis combrayicus* Croitor, 2020 (from the Late Pleistocene of France).

Theoretical significance. The results obtained from this study shed light on the emergence and development of the Palearctic biogeographic realm in the western part of Eurasia and North Africa. The investigation of deer antler evolution, ecomorphology, and functional morphology helped to establish the link between antler morphology and social behavior and environmental conditions. The systematic and morphological analyses provided insights into the systematic position of holometacarpal deer, leading to a reconsideration of some taxonomic groups at the family level. The study also revealed the significance of southern glacial refugia in the evolution and diversification of fossil cervids, and highlighted the general ecological and evolutionary strategy of the family Cervidae as the main mechanism for extinctions of fossil deer.

The applicative importance of the thesis: The results obtained from this study provide insights into the mechanisms by which climate change has influenced the systematic diversity and extinctions of cervid species in the past. The revealed origins and systematic positions of fossil cervids enable us to correlate their dispersals and evolution with major geological events and utilize them as biostratigraphic markers. Additionally, the findings on the systematics and phylogeny of fossil cervids allow us to gain a better understanding of the origin of the systematical diversity of modern species and the status of some threatened modern deer.

The main scientific results presented:

1. The Late Miocene holometacarpal deer from western Eurasia represent an early evolutionary stage of the telemetacarpal deer (subfamily Capreolinae).

2. The subfamily Pliocervinae is an artificial, polyphyletic taxonomic group at the family level that should be abandoned.

3. The early evolutionary radiation of the subfamily Capreolinae occurred in western Eurasia during the Late Miocene.

4. The first Pliocene plesiometacarpal deer from western Eurasia represent the early evolutionary radiation of the subfamily Cervinae from Southeast Asia.

5. The tribe Megalocerotini Viret, 1961 (= Megacerini Viret, 1961) is a polyphyletic group

that includes large-sized forms belonging to distant and unrelated phylogenetic branches.

6. The evolution of antlers in Palearctic deer follows a similar pattern of parallel morpho-functional adaptations that reduce health damage, wounding, and mortality during the rutting season.

7. The general ecological and evolutionary strategy of the family Cervidae is one of the most common causes of species extinction in Palearctic deer in the past, via the mechanism of ecological exclusion.

Implementation of scientific results. The results obtained regarding the systematics, evolution, and dispersal of fossil deer in the western Palearctic have been utilized for various purposes such as biostratigraphic regional correlations in the Republic of Moldova and Romania (Croitor et al., 2020; Terhune et al., 2020), studies of paleobiogeographic changes in Europe influenced by climate changes (Croitor, 2017), paleoecological reconstructions (Kaizer and Croitor, 2004; Curran et al., 2021), and analysis of the paleoecological and paleobiogeographic context of early hominin dispersals and subsistence in Europe (Croitor, 2017; Croitor et al., 2019).

Approval of scientific results. The main results and conclusions of the thesis were presented and discussed at 16 national and international conferences.

Publications on the topic of the thesis. The results of the thesis have been disseminated through 70 publications, comprising 1 monograph, 2 book chapters, 29 articles in international scientific journals with impact factor, 15 articles in recognized foreign scientific journals, 10 articles in national journals registered in the National Register of Specialized Journals, 4 articles in scientific collections, 22 abstracts presented at international scientific conferences, and 4 abstracts presented at national scientific meetings.

The volume and structure of the work. The dissertation comprises six chapters (including the introduction, methodology, list of abbreviations, systematic description, discussion, totaling 208 pages of main text) and cites 348 bibliographic sources.

Keywords: mammals, deer, Late Miocene, Pliocene, Pleistocene, taxonomy, systematics, evolution, phylogeny, paleobiogeography.

THESIS CONTENT

INTRODUCTION. The brief description of the study includes the following: a statement of the relevance and significance of the problem addressed, the research's purpose and objectives, the research hypothesis, the scientific novelty and practical implications of the results obtained, the validation of the research findings, and a summary of the thesis sections.

1. HISTORICAL OVERVIEW AND CURRENT STATE OF KNOWLEDGE ON THE CERVID SYSTEMATICS AND PHYLOGENY

This section of the thesis provides a bibliographic review that traces the evolution and changes in viewpoints on cervid taxonomy and systematics. The objective is to identify the causes of contradictory opinions and to highlight the main unresolved issues in the taxonomy and systematics of fossil deer from the western Palearctic. Additionally, this chapter presents the findings of recent studies in deer systematics, including molecular phylogeny.

2. RESEARCH MATERIAL AND METHODS

Holotypes and other species-type materials stored in the most significant paleontological collections of Europe are of central importance in this study. Special attention has been given to additional materials obtained from type localities and to craniological materials that were used in taxonomic studies at the genus level. The methodological approach adopted in this study is based on the application of neontological taxonomic criteria and rigorous taxonomic revision of fossil cervid taxa, including the revision of type specimens, nominotypical taxa, and nomenclatural acts. The main objective of this approach is to achieve taxonomic compatibility between fossil and modern deer taxa. Due to the limitations of the fossil record, the applied taxonomic criteria at the genus and species level rather correspond to "splitting" taxonomy (Croitor and Robinson, 2020). The morpho-functional analysis of diagnostic characters, particularly antlers, is applied to estimate their taxonomic value. The hierarchical clustering paired group algorithm UPGMA was computed using the Jaccard Similarity Index for presence-absence of diagnostic characters at the species, genus, and family levels. This clustering method is applied to estimate the systematic position of fossil deer taxa, including species and genera, among the modern representatives of the family Cervidae (Croitor, 2021).

3. SYSTEMATIC DIVERSITY OF TELEMETACARPAL DEER IN THE WESTERN PALEARCTIC

Family Cervidae Goldfuss, 1820

Subfamily Capreolinae Brookes, 1828

Genus *Lucentia* Azanza and Montoya, 1995

Type species. *Lucentia iberica* Azanza and Montoya, 1995.

Composition. *Lucentia iberica* Azanza and Montoya, 1995; *Lucentia pierensis* (Thomas, 1951).

Distribution. Late Miocene, Lower Turolian, (MN 11) (Azanza and Montoya, 1995).

Genus *Procapreolus* Schlosser, 1924

Type species: *Procapreolus latifrons* Schlosser, 1924 from the Late Tertiary of Mongolia.

Composition: *P. moldavicus* (Janovskaya, 1954) (Early Pliocene, Eastern Europe); *P. ucrainicus* Korotkevich, 1963 (Late Miocene, Ukraine); *P. florovi* Korotkevich, 1974 (final stage of Miocene, Ukraine); *P. pentelici* (Dames, 1883) (Mio-Pleistocene boundary, Greece); *P. vesti* Korotkevich, 1970 (Pliocene, North Caucasus); *P. cusanus* (Croizet and Jobert, 1928) (Late Pliocene, Western Europe); *P. stenos* Lin and Pan, 1978 (Early Pleistocene, China), *Procapreolus jinensis* Dong and Ye, 1996 (Late Miocene, Shanxi Province, China), *P. mongoliensis* (Vislobokova, 1983) (Pliocene, Mongolia).

Distribution: middle latitudes of Eurasia; Late Miocene to Early Pleistocene.

Genus *Pliocervus* Hilzheimer, 1922

Type species: *Cervus matheroni* Gervais, 1852.

Composition: the genus is monotypic.

Distribution: Late Miocene (early MN12) (de Bruijn et al., 1992), Western Europe.

Genus *Damacerus* Khomenko, 1913

Type species: *Damacerus bessarabiae* Khomenko, 1913.

Composition: the genus is monotypic.

Distribution: Late Miocene (MN12, Middle Turolian), Southeast Europe (Lungu and Rzebik-Kowalcka, 2011).

Genus *Metadicrocerus* Schlosser, 1924

Type species: *Procervus variabilis* Aleksejev, 1913.

Composition: the genus is monotypic.

Distribution: the Upper Miocene (MN12), southeast Europe.

Genus *Palaeaxis* Pohlig, 1911

Type species: *Cervus* (*Palaeaxis*) *loczyi* Pohlig, 1911.

Composition: the genus is monotypic.

Distribution: Late Miocene, Central Europe.

Genus *Capreolus* Frisch, 1775

Type species: *Cervus capreolus* Linnaeus (Linnaeus, 1766: p. 94).

Composition: *C. capreolus* (Linnaeus, 1766) (Late Pleistocene – Holocene, Europe); *C. constantini* Vislobokova and Kalmykov, 1995 (Pliocene, Trans-Baykal Area); *C. cuzanoides* Kahlke, 2001 (Early Pleistocene, Germany); *C. suessenbornensis* Kahlke, 1956 (Middle Pleistocene, Western Europe); *C. pygargus* Pallas, 1771 (modern, Siberia).

Distribution: Pliocene – Holocene of middle latitudes of Eurasia.

Genus *Neomegaloceros* Korotkevich, 1971

Type species: *Neomegaloceros gracilis* Korotkevich, 1971

Composition: the genus is monotypic.

Distribution: Late Miocene, Maeotian, MN 12, southern Ukraine.

Genus *Cervodama* Pidoplichko and Flerov, 1952

Type species: *Cervodama pontoborealis* Pidoplichko and Flerov, 1952

Composition: the genus is monotypic.

Distribution: Late Miocene - Pliocene, Southeastern Europe.

Genus *Croizetoceros* Heintz 1970

Type species: *Croizetoceros ramosus* (Croizet and Jobert, 1828)

Composition: the genus is monotypic.

Distribution: Pliocene – Early Pleistocene, Western Europe.

Genus *Alces* Gray, 1821

Type species: *Cervus alces* Linnaeus, 1758.

Composition: *A. alces* (Linnaeus, 1759) (Late Pleistocene – Holocene, boreal parts of

Eurasia and North America, America de Nord); *A. gallicus* (Azzaroli, 1952) (Early Pleistocene, Central Asia – Western Europe), *A. carnutorum* (Laugel, 1862) (late Early Pleistocene, Europe), *A. latifrons* (Johnson, 1874) (Muddle Pleistocene, middle latitudes of Eurasia).

Distribution: Pliocene - Holocene; North Eurasia and Northern America.

Genus *Rangifer* H. Smith, 1827

Type species: *Cervus tarandus* Linnaeus, 1758.

Subspecies: *Rangifer tarandus stadelmanni* Kahlke, 1963 (early Middle Pleistocene, Germany); *R. tarandus hibernicus* Scharff et al., 1917 (Late Pleistocene, Ireland); *R. tarandus tournalii* (De Serres, 1829) (Late Pleistocene, France); *R. tarandus constantini* Flerov, 1934 (Late Pleistocene, Siberia, Eastern Europe, possibly Western Europe)

Other species: *Rangifer sp*. from the Early Pleistocene of Isakovka-4 (Omsk, Russia) dated back to 2.1-1.8 Ma (Bondarev et al., 2017).

Distribution: early Middle Pleistocene – Holocene (van Kolfschoten et al., 2011); circumboreal geographical distribution.

4. SYSTEMATIC DIVERSITY OF PLESIOMETACARPAL DEER IN THE WESTERN PALEARCTIC

Subfamily Cervinae Goldfuss 1820

Genus *Praemuntiacus* Croitor, Zakharov and Mararescul, 2020

Type species: *Eostyloceros pidoplitschkoi* Korotkevich, 1964

Composition: *Praemuntiacus pidoplitschkoi* (Korotkevich, 1964) (Pliocene, Europe); *Praemuntiacus triangularis* (Zdansky, 1925) (Late Tertiary, China).

Distribution: Pliocene, Europe (Ukraine, Moldova, Poland, Slovakia, Bulgaria, Italy), Late Tertiary, Asia (China).

Genus *Metacervocerus* Dietrich, 1938

Type species: *Cervus pardinensis* Croizet and Jobert, 1828.

Composition: *M. pardinensis* (Croizet and Jobert, 1828) (Pliocene, Europe); *M. rhenanus* (Dubois, 1904) (Early Pleistocene, Europe); *M. shansius* (Teilhard de Chardin and Trassaert, 1937) (Early Pleistocene, China); *M. punjabiensis* (Brown, 1926) (Early Pleistocene, Siwaliks).

Distribution: Pliocene – Early Pleistocene of Eurasia.

Genus *Praeelaphus* Portis, 1920

Type species: *Cervus perrieri* Croizet and Jobert, 1828.

Composition: *P. perrieri* (Croizet and Jobert, 1828) (Pliocene, Western Europe); *P. lyra* (Azzaroli, 1992) (Pliocene, Italy); *P. warthae* (Czyżewska, 1968) (Early Pliocene, Poland); *P. australorientalis* Croitor, 2017 (Early Pliocene, Ukraine); *Praeelaphus sp.* (Early Pleistocene, Olivola, Italy); *P. messinae* (Pohlig, 1909) (Middle Pleistocene, Sicily).

Distribution: Pliocene – Early Pleistocene of Transcaucasia and Middle Pleistocene of Sicily.

Genus *Rucervus* Hodgson, 1838

Subgenus *Arvernoceros* Heintz, 1970

Type species. *Cervus ardei* Croizet and Jobert, 1828.

Composition: *R.* (*Arvernoceros*) *ardei* (Croizet and Jobert, 1828) (Pliocene, Europe); *R.* (*Arvernoceros*) *radulescui* Croitor, 2018 (Early Pleistocene, Romania); *R.* (*Arvernoceros*) *verestchagini* David, 1992 (Early Pleistocene, Moldova and Crimea); *Rucervus sp.* from Venta Micena-2 (Early Pleistocene, Spain).

Distribution. Early Pliocene–Early Pleistocene, western Eurasia.

Subgenus *Rucervus* Hodgson, 1838

Type species. *Cervus elaphoides* Hodgson, 1835, a junior synonym of *Cervus duvaucelii* Cuvier, 1823.

Composition: *R. duvaucelii* (Cuvier, 1823) (Middle Pleistocene – Holocene, South Asia); *R. simplicidens* (Lydekker, 1876) (Siwaliks, Early Pleistocene); *R. colberti* (Azzaroli, 1954) (Siwaliks, Early Pleistocene); *R. gigans* Croitor, 2018 (Early Pleistocene, Greece).

Distribution. Pliocene–Holocene, Southern Eurasia.

Genus *Haploidoceros* Croitor, Bonifay and Brugal, 2008

Type species: *Eucladoceros mediterraneus* M.-F. Bonifay, 1967.

Composition: the genus is monotypic

Distribution. Middle and Late Pleistocene, Southwestern France and the Iberian Peninsula.

Genus *Sinomegaceros* Dietrich, 1933

West Palearctic species: *Sinomegaceros stavropolensis* (Titov and Shvyreva, 2016) (Early Pleistocene of Stavropol, North Caucasus); *Sinomegaceros insolitus* (Vekua, Bendukidze and Kiladze, 2010) (Early Pleistocene of Dmanisi, Georgia).

Distribution. Pleistocene, Eurasia.

Genus *Eucladoceros* Falconer, 1868

Type species: *Cervus* (*Eucladoceros*) *sedgwickii* Falconer, 1868, a junior synonym of *Cervus dicranios* Nesti, 1841.

Composition: *Eucladoceros dicranios* (Nesti, 1841) (Early Pleistocene, Europe); *Eucladoceros ctenoides* (Nesti, 1841) (Early Pleistocene, Europe); *Eucladoceros boulei* (Teilhard de Chardin and Piveteau, 1930) (Early Pleistocene, China); *Eucladoceros proboulei* Dong and Ye, 1996 (Pliocene, China).

Distribution: Pliocene - Early Pleistocene, Eurasia.

Genus *Praemegaceros* Portis, 1920

Subgenus *Praemegaceros* Portis, 1920

Type species: *Cervus dawkinsi* Dawkinsi, 1882.

Composition: *P.* (*Praemegaceros*) *dawkinsi* (Dawkinsi, 1882) (Middle Pleistocene, England); *P.* (*Praemegaceros*) *obscurus* (Azzaroli, 1953) (Early Pleistocene, Transcaucasia, Near East, Europe), *P.* (*Praemegaceros*) *mosbachensis* (Soergel, 1927) (Middle Pleistocene, Western Europe).

Distribution: Early and Middle Pleistocene of Western Eurasia.

Subgenus *Nesoleipoceros* Radulesco and Samson, 1967

Type species: *Cervus* (*Eucladoceros*) *cazioti* Depéret, 1897.

Composition: *P.* (*Nesoleipoceros*) *sp.* from Pietrafitta (Early Pleistocene, Italy); *P.* (*Nesoleipoceros*) *solilhacus* (Robert, 1830) (final Early Pleistocene – Middle Pleistocene, Europe); *P.* (*Nesoleipoceros*) *sardus* (van der Made and Palombo, 2005) (Middle Pleistocene, Sardinia); *P.* (*Nesoleipoceros*) *sp.* from Su Fossu (Middle Pleistocene, Sardinia); *P.* (*Nesoleipoceros*) *rossii* (Pereira, 2001) (Late Pleistocene, Corsica), *P.* (*Nesoleipoceros*) *cazioti* (Depéret, 1897) (Late Pleistocene, Corsica and Sardinia).

Distribution: Early Pleistocene – Late Pleistocene, Europe, Corsica, Sardinia.

Subgenus *Orthogonoceros* Kahlke, 1956

Type species: *Cervus verticornis* Dawkins, 1872.

Composition: *P.* (*Orthogonoceros*) *verticornis* (Dawkins, 1872) (Middle Pleistocene, Europe); *P.* (*Orthogonoceros*) *pliotarandoides* (De Alessandri, 1903) (Early Pleistocene, Europe, Central Asia).

Distribution: Early and Middle Pleistocene, Europe, Central Asia.

Genus *Candiacervus* Kuss, 1975

Type species: *Anoglochis cretensis* Simonelli, 1907.

Composition: *Candiacervus cretensis* (Simonelli, 1907) (Pleistocene, Crete); *C. rethymnensis* Kuss, 1975 (Pleistocene, Crete); *C. cerigensis* Kuss, 1975 (Pleistocene, Crete); *C. pigadiensis* Kuss, 1975 (Pleistocene, Crete); *C. ropalophorus* de Vos, 1984 (Pleistocene-Holocene, Crete); *C. devosi* van der Geer, 2018 (Pleistocene, Crete); *C. listeri* van der Geer, 2018 (Pleistocene, Crete); *C. reumeri* van der Geer, 2018 (Pleistocene, Crete).

Distribution: Middle-Late Pleistocene and Holocene of Crete, Kasos, and Karpathos.

Genus *Cervus* Linnaeus, 1758

Type species: *Cervus elaphus* Linnaeus, 1758.

Composition: *C. elaphus* Linnaeus, 1758 (Middle Pleistocene – Holocene, Eurasia); *C. canadensis* Erxleben, 1777 (Middle Pleistocene – Holocene, Eurasia and North America); *C. nestii* Azzaroli, 1947 (Early Pleistocene, Italy and Georgia); *C. magnus* (Zdansky, 1925) (Early Pleistocene, Eastern Asia); *C. nippon* Temminck, 1838 (Pleistocene – Holocene, Eastern Asia); *C. astylodon* (Matsumoto, 1926) (Late Pleistocene, Ryukyu Islands).

Distribution: Early Pleistocene – Holocene, Eurasia, North Africa, and Northern America.

Genus *Praedama* Portis, 1920

Type species. *Cervus savini* Dawkins, 1885.

Composition: *Praedama savini* (Dawkins, 1885) (Middle Pleistocene, Western Europe); *P. novocarthaginiensis* (van der Made, 2014) (late Early Pleistocene, the Iberian Peninsula); *P. matritensis* (van der Made, 2018) (Late Pleistocene, the Iberian Peninsula); *P. dupuisi* (Stehlin, 1912) (final stage of Early Pleistocene, France); *P. giulii* (Kahlke, 1997) (late Early Pleistocene, Central and Eastern Europe).

Distribution: Early Pleistocene – Late Pleistocene, Europe.

Genus *Leptocervus* Capasso Barbato, 1990

Type species: *Cervus major* Capasso Barbato and Petronio, 1986

Composition: *Leptocervus major* (Capasso Barbato and Petronio, 1986); *Leptocervus dorothensis* Capasso Barbato, 1990.

Distribution: Upper Pleistocene, Crete.

Genus *Megaloceros* Brookes 1828

Type species: *Alce gigantea* Blumenbach, 1799.

Composition: *Megaloceros giganteus* (Blumenbach, 1799) (Middle Pleistocene to Holocene, middle latitudes of central and western Eurasia); *Megaloceros mugharensis* (di Stefano, 1996) (Middle Pleistocene, Near East).

Distribution: Middle Pleistocene – Holocene, Southern Siberia and Kazakhstan, Near East, Europe.

Genus *Megaceroides* Joleaud, 1914

Type species: *Cervus algericus* Lydekker, 1890

Composition: *Megaceroides algericus* (Lydekker, 1890); the genus is monotypic.

Distribution: Late Pleistocene – Holocene, North Africa.

Genus *Dama* Frisch, 1775

Type species: Cervus dama Linnaeus, 1758

Composition: *Dama eurygonos* Azzaroli, 1947 (Early Pleistocene, Italy); *Dama vallonnetensis* (de Lumley, Kahlke, Moigne and Moulle, 1988) (late Early Pleistocene, Europe); *Dama clactoniana* Falconer, 1868 (Middle Pleistocene, Western Europe); *Dama carburangelensis* (De Gregorio, 1925) (Pleistocene, Sicily); *D. dama* (Linnaeus, 1758) (Late Pleistocene - Holocene, Mediterranean Europe and Anatolia); *D. mesopotamica* Brooke, 1875 (Late Pleistocene - Holocene, Near East).

Distribution: Early Pleistocene – Holocene, Near East, Europe.

5. MAIN EVOLUTIONARY FEATURES OF CROWN CERVIDS FROM THE WESTERN PALEARCTIC

5.1. Functional morphology of Palearctic Cervinae antlers

According to Davitashvili (1961), the branched and complicated antlers of advanced cervids represent a specific adaptation that "softens" sexual selection and reduces excessive male mortality during intraspecific combats. The most proximal antler tine, the brow tine, serves a function of locally restricted protection of the eyes and face during combats, and is present very early in cervid evolution (Lister, 1987). The second proximal tine, the bez tine, is unique to *C. elaphus* and *C. canadensis* and appeared during the early Middle Pleistocene, coinciding with a significant increase in body size in the *Cervus* lineage. The estimated body mass of the primitive small-sized *C. nestii* was around 60 kg (Croitor, 2018b), while the body mass of the most ancient subspecies of red deer *C. elaphus acoronatus* was approximately 237 kg (estimated based on occipital height, including cranial material from the Tiraspolian gravel and specimens studied by Di Stefano and Petronio, 1992; sample size =14). Thus, a four-fold increase in body size is observed in the *C. nestii* - *C. elaphus* lineage during the Early Pleistocene - early Middle Pleistocene transition. Petrie (1988) suggested that the costs of intraspecific combats may be relatively greater for larger animals, which may have a greater capacity to injure each other. This may explain why red deer and wapiti developed the second basal tine, enhancing facial protection during combats. It is interesting to note that the bez tine tends to diminish in European red deer during the Late Pleistocene and Holocene, concurrently with body size reduction (Lister, 1987). Nevertheless, the direct relationship between body size and the strength of the bez tine in red deer cannot be considered proven, since the bez tine is relatively weak in the largest modern red deer subspecies, *C. elaphus maral* (Heptner and Zalkin, 1947; Flerov, 1952). Lister proposed that the reduction of the bez tine in red deer is correlated with the development of a richly branched antler crown, but the example of *C. elaphus maral* does not support this hypothesis.

In turn, the middle tine (or trez tine) appears early in the evolution of the Cervinae subfamily as a second ramification and coincides with the increase in body size and the reduction of upper canines, making male antlers the only dangerous weapon against conspecific rivals (Geist, 1971). The development of this tine in the early stages of cervid evolution also increased the safety of combatting stags that reached a certain body mass threshold, increasing the risk of lethal wounding. Kitchener (1987) suggested the trez tine's protective function against a rival's antlers for cervids that bear highly evolved and complicated antlers, such as red deer and giant deer. Davitashvili (1961) demonstrated the importance of additional antler tines in red deer stags with degenerated and simplified antlers that could easily wound and kill their conspecific rivals. A forwardly pointed tine situated in the middle of the antler beam appeared several times independently in the evolution of cervines. For example, the middle tine of *Praemegaceros* verticornis from the Middle Pleistocene of

Europe, which appeared relatively late in the *Praemegaceros* lineage, is completely absent in *P. pliotarandoides* from the late Early Pleistocene (Croitor, 2006). Although the middle tine of *P. verticornis* is analogous to the trez tine of *C. elaphus* and *C. canadensis* and most likely had the same function of locking a rival's antlers, it is not homologous since its evolutionary history is different. The evolutionary importance of the middle tine may be confirmed by the fact that many insular dwarfed deer with diminished and simplified antlers maintain the middle tine, which may be the only remaining antler branch in extreme cases of antler simplification (Azzaroli, 1961; van der Geer, 2018).

It is important to note that the trez tine or its analogues typically evolved in cervids from middle latitudes and are absent in southern lineages with large antlers, such as *Rucervus* and *Panolia*. One possible explanation is that male survival in cervids from temperate latitudes with cold winters and seasonal drops in forage is exposed to greater pressure. Seasonal male mortality, particularly among young and prime-adult age deer, is important (Clutton-Brock et al., 1982), and additional security adaptations in antler shape can reduce excessive male loss during combats, compensating for seasonal male mortality. Therefore, a direct relationship between harder environmental conditions with seasonal drops in temperature and forage availability and richly branched antlers can be assumed. The consequences of seasonality in southern latitudes are less costly for deer stags, which may explain the smaller number of ramifications and the absence of the "second-level protection" tine (the trez tine or its analogues) in large South Asian deer species.

Deer adapted to open landscapes typically have a posterior tine situated on the back side of the antler, below the crown part (Croitor, 2018). The posterior tine appears independently in several cervid lineages of the Cervinae and Capreolinae subfamilies, including *Rangifer*, *Megaloceros*, *Praemegaceros*, *Praedama*, *Sinomegaceros*, and some species of the genus *Dama*. This tine is usually situated on the convex side of the antler bow, which is often sharply bent in this area. In some cases, the lowermost posterior crown tine may be very large, strong, and detached from the palmation, as seen in *Dama geiselana* and *D. clactoniana* (Leonardi and Petronio, 1976; Pfeiffer, 1998).

The development of the posterior tine is not dependent on body size and is not correlated with other parts of the antlers. Its stability within the individual variation range suggests an important evolutionary selection in favor of this character, which appeared repeatedly and independently in several lineages of the family Cervidae.

The most plausible explanation for the iterative development of the posterior tine during cervid evolution is its specific function as a defense against ectoparasites in rutting males. Studies of North American deer and territorial African antelopes have shown that males' involvement in rutting decreases their behavioral and immune defense against ticks, which can distract them from the rutting behavior and damage their physical and health state (Hart, 1997; Mooring et al., 2004).

Rutting males have a greater parasite load than non-rutting males, which is attributed to the elevated testosterone levels that suppress grooming behavior and increase vigilance. This increased ectoparasite burden is a frequent side effect in rutting males, as observed in male white-tailed deer (Main et al., 1981) and rutting impala males (Hart, 1997).

The posterior tine in cervids is a specialized adaptation for scratch grooming in rutting males, which indirectly increases their combat capacities (Croitor, 2016). The acquisition of this tine has indirectly influenced mating success by diminishing the ectoparasite burden and improving the vigilance and physical state of rutting stags.

According to available bibliographic data, ectoparasites can have a significant disturbing effect duting the rutting period. Observations of modern North American wapiti show that September and October are the peak times for feeding by larvae of the winter tick *Dermacentor albipictus* (Mooring and Samuel, 1998). This stage of the parasite's biological cycle coincides with the rutting season in elaphine deer (Flerov, 1952; Sokolov, 1959), and therefore has a significant negative influence on the physical state and rutting success of stags. While the use of antlers for scratch grooming is rarely reported in modern cervids, which are mostly adapted to wooded and ecotone habitats (Mooring et al., 2004), it is recorded in tundra reindeer (*Rangifer tarandus tarandus*), the only modern deer adapted to open environments (Kynkäänniemi et al., 2014), indicating the importance of this behavior for mitigating the effects of ectoparasites.

5.2. Multivariate analysis of craniodental characters and phylogenetic relationships

Unlike the subfamily Cervinae, which exhibits a wide range of antler forms, most representatives of the subfamily Capreolinae are characterized by a generally conservative three-pointed antler type (Croitor, 2021). This antler morphology is observed in modern roe deer (*Capreolus capreolus*) and is recognizable in practically all evolutionary lineages, except for forms that have undergone secondary antler simplification, such as *Mazama* and *Pudu*. The initial *Capreolus*-like antler structure is characterized by the very high position of the first ramification and the bifurcation of the posterior branch that forms two more or less equally sized tines. This initial structure is characteristic of *Procapreolus*, *Capreolus*, and *Eocoileus* (Fig. 1) and was termed by Lydekker (1898) as the “forked type of antlers”. According to Samejima and Matsuoka (2020), the morphological elements of the three-pointed antlers (the first tine, the distal fork) of Cervinae and Capreolinae are structurally different and not homologous. It seems that the evolutionary potential of the two distal ramifications is equal since one can find within Capreolinae the evolutionary specializations with a stronger development of the posterior branch (*Pliocervus*, *Pavlodaria*, *Alces*) or the structure with stronger development of the anterior branch (*Capreolus*, *Procapreolus*, *Odocoileus*, *Rangifer*, *Neomegaloceros*).

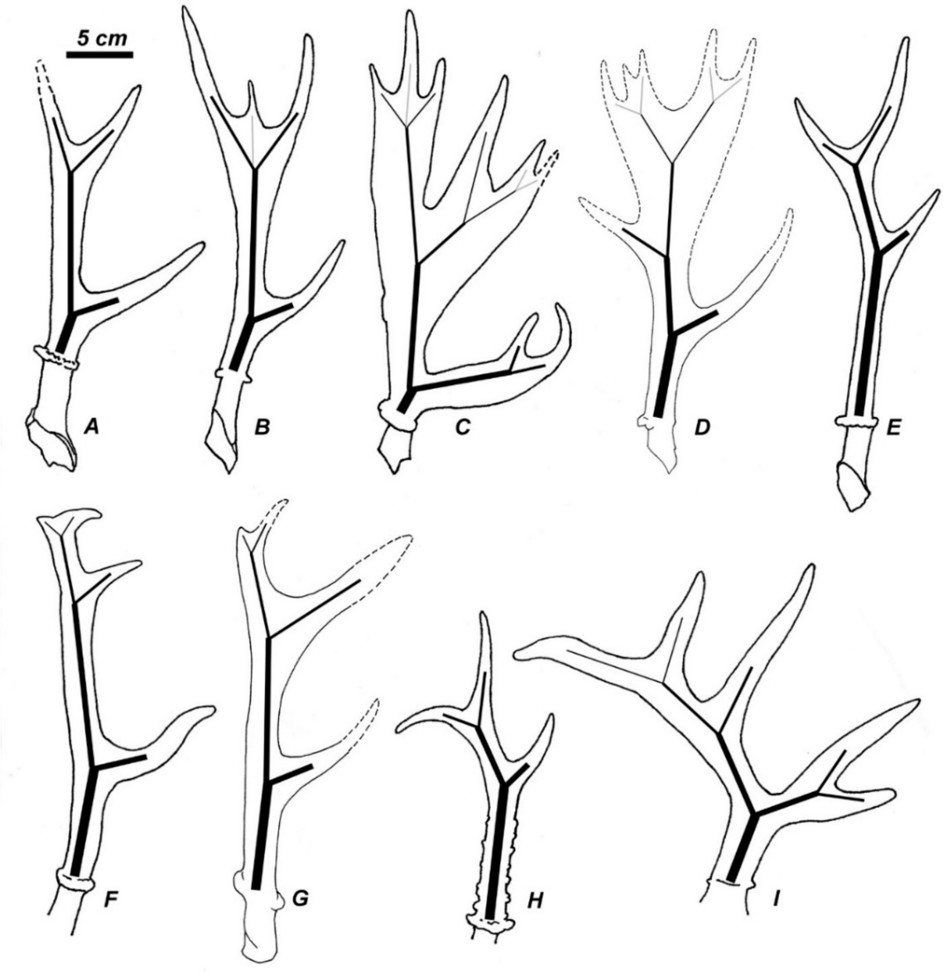

Fig. 1. The antler bauplan of Capreolinae: A, *Eocoileus gentriorum* from the Pliocene of North America (adapted from Webb 2000); B, *Damacerus bessarabiae* from the Late Miocene of Southeastern Europe (adapted from Khomenko 1913); C, *Metadicrocerus variabilis* from the Late Miocene of Southeastern Europe (adapted from Aleksejev 1915); D, *Neomegaloceros gracilis* from the Late Miocene of Southeastern Europe (partial reconstruction); E, *Procapreolus moldavicus* from the Early Pliocene of Southeastern Europe (adapted from Korotkevich 1970); F, *Pliocervus matheroni* from the Late Miocene of Western Europe (adapted from Dawkins 1878); G, *Pavlodaria orlovi* from the *Hipparion* fauna of Kazakhstan (adapted from Vislobokova 1980); H, *Capreolus capreolus* (adapted from Danilkin 1999); I, *Alces alces* (adapted from Sokolov 1959)

The conservative nature of antler evolution in Capreolinae has traditionally been interpreted as evidence of its more primitive status relative to Cervinae (Czyżewska, 1968). However, a more appropriate interpretation is that there are two distinct patterns of antler evolution and development within the family Cervidae (Samejima and Matsuoka, 2020). The character of diversity of antlers among telemetacarpal deer is the result of a limited number of variations in antler branch bifurcations.

The general antler structure and specific antler morphology suggest that the Late Miocene "Pliocervines" from Europe are closely related to modern representatives of the subfamily Capreolinae. All of these deer share a basic *Capreolus*-like antler structure, which can even be recognized in the highly specialized *Metadicrocerus variabilis* and modern *Alces alces* (Fig. 1).

Brooke (1878) previously described the antler structure of *Alces* as dichotomous and noted its similarity to *Blastocerus dichotomus*. In all of the mentioned cases, the first tine is relatively high, and the distal parasagittal fork is consistently present. This fork is clearly visible in *Damacerus bessarabiae* and *Metadicrocerus variabilis*, and it marks the end of the palmation formed by the extension of the second beam segment. Fully-grown antlers of *D. bessarabiae* have an accessory distal tine in addition to the distal fork, while in *M. variabilis*, each tine of the distal fork is bifurcated or trifurcated (Fig. 1C).

A multivariate analysis based on craniodental characters (including antlers) and some postcranial features has placed the extinct Old World genera *Metadicrocerus*, *Damacerus*, *Pliocervus*, *Procapreolus*, and *Lucentia* among the selected modern capreolines. *Lucentia iberica*, a peculiar small-sized cervid from the Late Miocene of the Iberian Peninsula (MN11), is characterized by simple two-pointed antlers with a high position of the bifurcation and a specific dental morphology (molarized P_4, upper molars supplemented with protoconal fold, lower molars with *Palaeomeryx* fold) (Azanza and Montoya, 1995). The similarity of *Lucentia* antlers with those of *Capreolus* and European "Pliocervines" has been noted by Azanza and Montoya (1995), who assumed that the Iberian deer could represent an evolutionary stage preceding the dichotomy of cervines and capreolines. However, the cuted authors placed *Lucentia* closer to *Cervinae*. In my opinion, the emerging protoconal fold in the upper molars of *Lucentia iberica* should be regarded as an important diagnostic apomorphy of the telemetacarpal deer. Therefore, while *L. iberica* represents the most primitive two-pointed stage of antler evolution of *Capreolinae*, its dentition is already quite specialized, shoing the main morphological features of telemetacarpal deer.

It is possible that the cervid described by Azanza (2000) as "Muntiacinae gen. et sp. indet." from the Early Turolian of Crevillente-2 (Alicante, Spain) represents a more primitive form of the early capreoline evolutionary diversification. This cervid is characterized by a small size similar to modern muntjacs. However, its dental morphology displays advanced characteristics such as the emerging protoconal fold and labiolingually narrowed crowns of upper molars, which are correlated with the evolutionary trend towards mesodont specialization (Croitor et al. 2020).

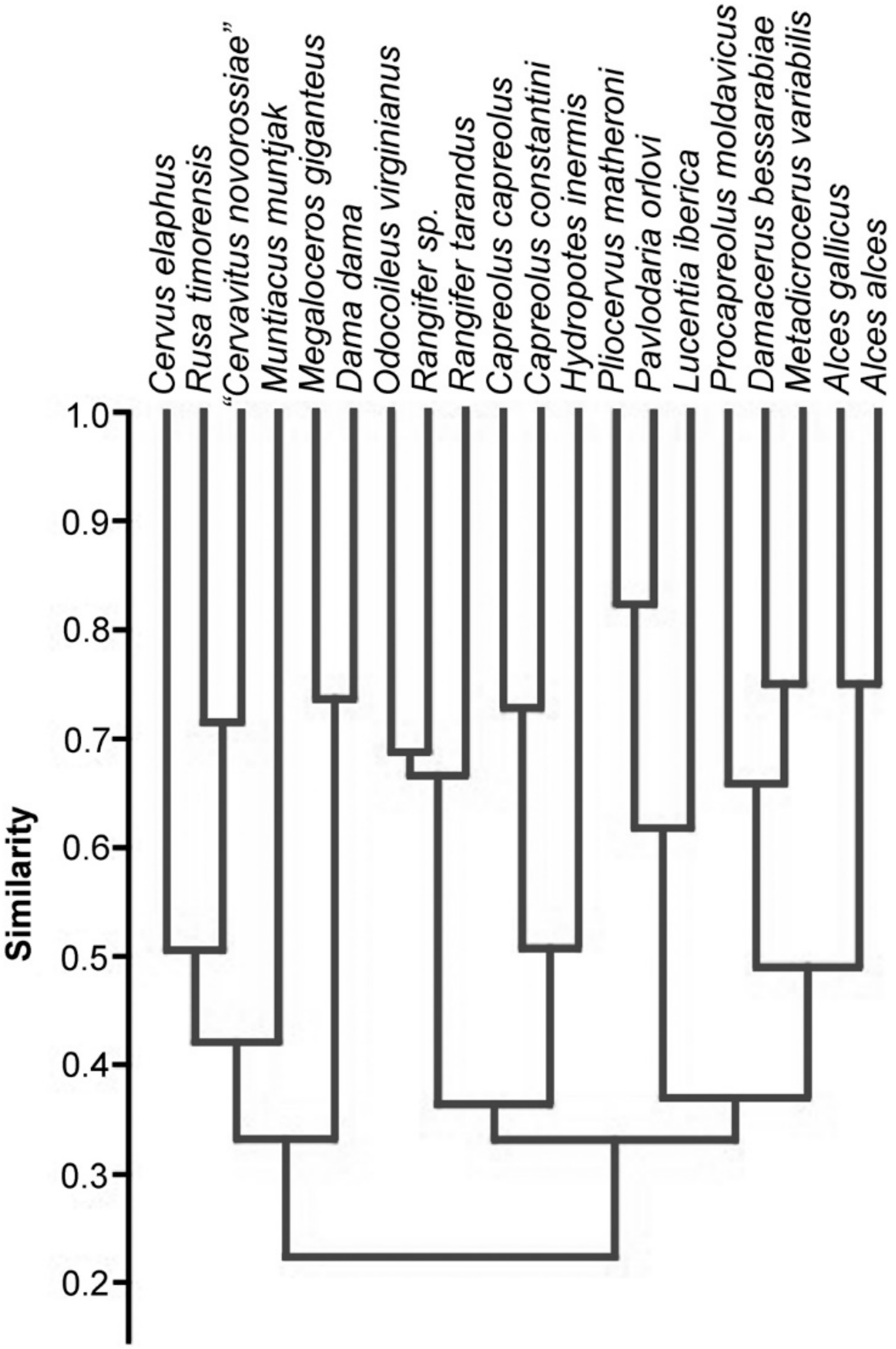

Fig. 2. Cluster analysis of the diagnostic antler, cranial, dental, and some postcranial characters of the Late Miocene “pliocervines” and selected modern and extinct representatives of the subfamilies Capreolinae and Cervinae. The data on “*Cervavitus novorossiae*” from the Late Tertiary of China are adapted from Zdansky (1925). The cophenetic correlation coefficient is 0.823

The cervid from Crevillente-2, tentatively assigned to the subfamily Muntiacinae, exhibits dental features that are more advanced than those found in muntjacs, such as high-crowned upper molars with an emerging protoconal fold. This dental morphology is similar to that of capreolines and suggests that this cervid may represent an early, "muntjac-like" stage in the evolution of Capreolinae.

We currently lack information on the antler features and cranial morphology of the deer found in Crevillente-2.

The multivariate analysis groups *Lucentia iberica* with *Pliocervus matheroni* and *Pavlodaria orlovi*, and this unexpected cluster is not contradictory (Fig. 2). *Pliocervus* and *Pavlodaria* evolved a less common antler bauplan among Capreolinae, with further bifurcation of the posterior branch of the initial distal fork (Fig. 2). Therefore, it can be assumed that the antler bauplan of *Pliocervus* and *Pavlodaria* evolved independently from a cervid form with two-pointed antlers similar to Lucentia.

It's important to note that the further bifurcation of the anterior or posterior branch of the initial distal bifurcation in many cases could represent a parallelism in the evolution of Capreolinae and should not be regarded as an important systematic character. *Lucentia iberica* shares with *Pliocervus matheroni* the subtriangular cross-section of the distal portion of the antler; however, the Iberian cervid cannot be considered a forerunner of *Pliocervus*, as it already shows advanced molarization of P_4.

Procapreolus, a Capreolinae cervid with three-pointed antlers, is considered to be one of the less-specialized genera. Some of its features, such as the long pedicles, short nasal bones, large preorbital pits, and large upper canines, are reminiscent of muntiacines, but its basicranial morphology and specialization of cheek teeth, including the *Palaeomeryx* fold, strong protoconal fold in upper molars, and advanced molarization of P_4, firmly place it within Capreolinae. *Lucentia pierensis*, which shares some morphological features of two-pointed antlers, such as the cylindrical antler axis and sub-rectangular antler cross-section in the area of ramification, is most likely similar to *Procapreolus*. However, due to the lack of available information on its craniodental morphology, it was not included in the analysis. The genera *Damacerus* and *Metadicrocerus* are closely related to *Procapreolus*, sharing most of the primitive features combined with typical Capreolinae characteristics, including the *Capreolus*-like antler bauplan. *Turiacemas concudensis* from the Late Miocene of the Iberian Peninsula may also be related to *Damacerus* and *Metadicrocerus* based on its sub-rectangular cross-section of the antler in the area of the first ramification and the triangular shape of the cross-section of the first tine

The genera *Procapreolus*, *Damacerus*, and *Metadicrocerus*, along with *Turiacemas* (possibly), represent the Late Miocene evolutionary radiation of cervids with a *Capreolus*-like antler bauplan. *Neomegaloceros gracilis* (Fig. 1D) and *Palaeaxis loczyi* Pohlig, 1911 also belong to the evolutionary radiation of the telemetacarpal deer from Eastern Europe. *N. gracilis* is a rather advanced deer with short and anteroposteriorly compressed pedicles and a very high position of the first ramification. The study of the type specimen cast (Natural Histiry Museum of Kyiv) revealed the particular shape of the partially destroyed distal antler portion that extends into a bilobed palmation that terminates in four or five distal tines, according to Korotkevich (1971). The cross-section of the first tine is triangular, as in *Damacerus* and *Metadicrocerus*. The antler of *N. gracilis* bears a well-developed posterior tine, which may be homologous to the posterior tine in *Capreolus*-like antlers.

The genus *Alces* is part of the Late Miocene radiation of Capreolinae in Europe. However, the earliest reported occurrence of elks is in the Pliocene of the Trans-Baikal Area (Vislobokova et al., 1995). The extinct European Mio-Pliocene capreolines share several features with modern elks, such as the general antler bauplan, the incomplete division of nasal cavities by the sagittal plate of the vomer, the presence of the *Palaeomeryx* fold (which is still present in *Alces gallicus*), the development of the protoconal fold in upper molars, the rectangular shape of the beam cross-section below the palmation, and the development of additional antler prongs and tine bifurcations. However, *Damacerus* and *Metadicrocerus* cannot be considered probable ancestors of *Alces*, because unlike *Alces*, they are characterized by some advanced morphological features, such as the caudal extension of nasal bones until the imaginary line connecting the anterior edges of orbits. The geographic center of elk evolution is most likely in the eastern regions of Eurasia, where the earliest remains of *Alces* have been found (Vislobokova et al., 1995).

Alces gallicus has been considered as the most primitive direct ancestor of modern elks and standing at the base of the elk evolutionary lineage (Azzaroli, 1952; Heintz and Poplin, 1981; Vislobokova, 1986; Lister, 1993; Boeskorov, 2001; Breda, 2001). The dentition of *A. gallicus* retains some primitive features, such as the *Palaeomeryx* fold in lower molars, unmolarized P_3, and the "*Cervus*-like" facial morphology (Azzaroli, 1952; Boeskorov, 2005; Croitor, 2018b). However, this species should be considered as a specialized side branch of elks, characterized by an important advanced cranial feature, the short braincase. The braincase breadth/bregma to inion length ratio in *A. gallicus* from East Runton (M6101, NHML) is 104.9%, indicating a rather short braincase proportion. In contrast, the same neurocranial index in *A. latifrons* from Mundesley (M6553, NHML) is 85.5%, indicating a primitive elongated proportion. The extremely elongated basal segment of antlers (between the burr and the first ramification) in *A. gallicus* is thus a far-reaching evolutionary specialization of the side phylogenetic branch, rather than an initial primitive feature of elk antlers. Therefore, the relative braincase length data does not support Boeskorov's (2005, 2006) view that *A. latifrons* is a giant descendant of *A. gallicus*. Nonetheless, I agree with Boeskorov (2005) that *A. latifrons* could not be a direct ancestor of modern *A. alces* due to the irreversibility of evolutionary specialization. Some poorly defined taxa from Southeastern Europe, such as *Pseudalces mirandus* Flerov, 1962, and Tamanalces caucasicus Verestchagin, 1957, are often reported as side evolutionary branches of elks (Vislobokova 1986, 1990; Boeskorov 2001, 2005, 2006). However, *T. caucasicus* from the final stage of the Early Pleistocene of the Taman Peninsula is a junior synonym of *Praemegaceros solilhacus* (Croitor, 2006), while *P. mirandus* from the Pliocene of Kosiakino is a giraffid (Croitor, 2018).

Cervodama pontoborealis Pidoplichko and Flerov, 1952 from Mariupol, belongs to the specialized Capreolinae deer of the Late Miocene evolutionary radiation of telemetacarpal deer. While its palmated antlers bear some superficial resemblance to those of modern *Alces* (Korotkevich, 1970; Vislobokova, 1990), the antler bauplan of *Cervodama pontoborealis* is not identical to that of *A. alces*. Unlike the elk of the modern type, the tines of the distal fork are stronger in *Cervodama pontoborealis* and do not form further dichotomous bifurcations.

5.3. Matching fossil record and molecular phylogeny data

Molecular phylogenetic analysis confirms the earlier broadly accepted viewpoint that the subfamily Cervinae, consisting of plesiometacarpal "Old World deer", is monophyletic (Pitra et al., 2004). This result was expected and supports the dichotomy of the family Cervidae described by Brooke (1878), who divided all cervids into the informal groups of Plesiometacarpalia and Telemetacarpalia. This dichotomy is also supported by modern molecular phylogenetic studies (Pitra et al., 2004; Gilbert et al., 2006).

According to Douzery and Randy (1997), the Capreolinae clade likely emerged between 8.7 and 10.4 Ma, which aligns with the chronologic distribution of archaic capreolines such as *Pliocervus matheroni* (MN 12-13, 5.3-8.2 Ma), *Procapreolus ucrainicus* (MN 11-12, 7.1-9.0 Ma), and *Palaeaxis loczii* (MN 10, 9.7 Ma) (Valli, 2010). Similar to Cervinae, the Late Miocene radiation of Capreolinae initially comprised a wide range of ecological and evolutionary forms such as *Metadicrocerus* with large palmed antlers and the *Muntiacus*-like *Procapreolus* from Eastern Europe, *Pliocervus* from Western Europe with large upper canines and four-tined antlers, and Pavlodaria from Kazakhstan with flattened four-tined antlers. While holometacarpal limbs with advanced reduction of proximal portions of lateral metacarpals are known for *Metadicrocerus* (Croitor, 2021), the holometacarpality of other Late Miocene cervids from Eastern Europe has not yet been demonstrated (Azanza et al., 2013).

The discovery of *Capreolus* in the Trans-Baikal region of Russia, specifically in Udunga (Vislobokova et al., 1995), suggests that the origin of roe deer occurred in the eastern part of the Palearctic. The emergence of *Alces*, on the other hand, may be linked to a cervid form similar to *Metadicrocerus variabilis*. This particular cervid is characterized by short, comparatively stronger divergent pedicles, and large antlers that tend to evolve palmations. According to Gilbert et al. (2006), the Capreolini+Alceini branch diverged around 7.4 million years ago, which coincides with the occurrence of *Metadicrocerus* in the Vallesian-Turolian of Moldova (MN 10-12, 7.1-9.5 Ma) (Petronio et al., 2007; Dong, 2011).

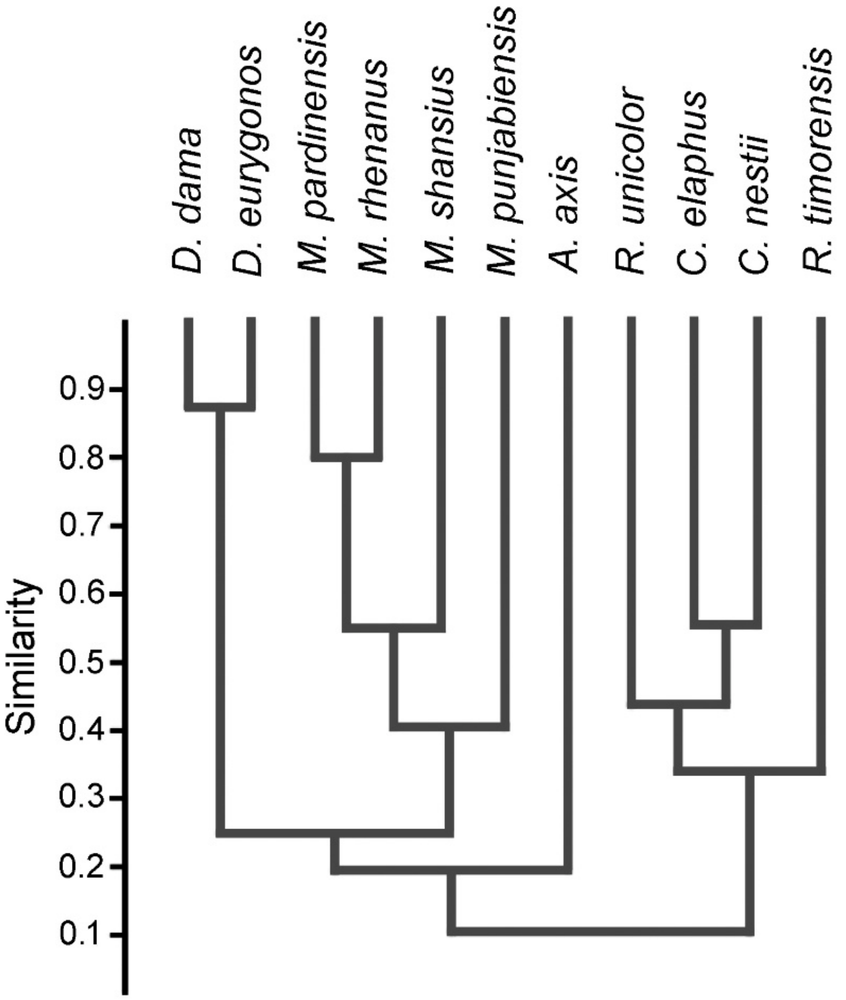

Fig. 3. Cluster analysis of the diagnostic cranial, dental, and antler characters of small-sized Cervinae from the Early Pleistocene of western Palearctic (the so-called "*Dama*-like deer") and selected modern and fossil cervid species from the Oriental Zoogeographic Realm. The cophenetic correlation coefficient is 0.9152

According to Douzery and Randi (1997), the divergences within Cervinae are thought to be older events, occurring from the Miocene to the Plio-Pleistocene epochs. This observation is consistent with the earliest arrival of Cervinae, which includes *Metacervocerus*, *Praeelaphus*, and *Rucervus*, during the Early Pliocene (MN15) in Eastern Europe (Croitor and Stefaniak 2009).

The divergence within the phylogenetic branch related to the genus *Cervus* is estimated to have occurred between 3.3 and 7.1 million years ago, while the divergence within the *Cervus elaphus* lineage is estimated to have occurred between 0.4 and 2.5 million years ago (Douzery and Randi, 1997). The early divergence within the *Cervus* phylogenetic branch, as proposed by Douzery and Randi (1997), may be supported by the early occurrence of *Cervus nestii* in the Early Pleistocene of Olivola and Upper Valdarno (Italy). The typical cranial morphology of modern red deer is already evident in this species (Croitor, 2006). Additionally, the frontal orientation of the distal antler fork is a distinguishing feature shared by *C. nestii* and the primitive subspecies *C.*

elaphus acoronatus, *C. elaphus bactrianus*, and *C. elaphus yarkandensis*.

The divergence of *Dama*, the only modern genus not known from Southeast Asia, from Cervus and related cervines from the Asian continent occurred quite early, during the Early Pliocene (Pitra et al., 2004) or around 3.0 Ma (Gilbert et al., 2006). This is consistent with the first occurrence of Cervinae in Western Eurasia, which likely led to the local evolution of the genus *Dama*. The most likely predecessor of *Dama* is the Early Pliocene *Metacervocerus pardinensis* from Eastern Europe, which is characterized by simple three-pointed antlers and a strong cingulum in upper molars (Fig. 3). The oldest record of *Dama* comes from the Early Pleistocene of the Upper Valdarno and Val di Chiana in Italy (Croitor, 2006).

6. PALEOBIOGEOGRAPHY OF DEER FROM THE WESTERN PALEARCTIC

6.1. Paleobiogeography of subfamily Capreolinae

The phylogenetic clade of modern Eurasian Capreolinae is significantly depleted due to the extinction of many evolutionary branches (Geist, 1998). This can be attributed to the fact that the adaptive radiation of Capreolinae occurred in the temperate latitudes of Eurasia, which were more affected by climate change. In contrast to the coeval Cervids from the Oriental evolutionary radiation, the Late Miocene “crown cervids” from Eastern Europe share a rather uniform morphology of dentition, indicating a different evolutionary path. Lower molars in all European and North Asian Late Miocene genera (*Procapreolus*, *Metadicrocerus*, *Pliocervus*, *Pavlodaria*) are reinforced with the *Palaeomeryx* fold, and the lower fourth premolar (P_4) has a trend towards early advanced molarization, in combination with a relatively long premolar series.

The paleobiogeographic history of telemetacarpal and plesiometacarpal deer may explain the morphological differences between Capreolinae and Cervinae. The evolutionary radiation of telemetacarpal deer in western Eurasia occurred in the conditions of the emerging Mediterranean biome during the Late Miocene. The biome of southwest Europe, where the highest diversity of primitive capreolines is found, gradually transitioned from mixed warm forests to the Mediterranean biome (Mosbrugger, 2008). The emergence of Mediterranean-type climates, triggered by the growth of the east Antarctic ice sheet and progressive global cooling, as suggested by Allen (1996) and Rundel et al. (2016), might explain this shift. Unlike cervines, capreolines did not have extensive refugia within the tropical climate latitudes, and all their evolutionary radiation evolved in rather dry biomes of Mediterranean type. Possibly, the telemetacarpal type of lateral metacarpal reduction is also linked to the cursorial adaptation in relatively dry environments with hard ground. The preserved articulations of lateral digits with the distal portions of the second and fifth metacarpals could be an adaptation to prevent displacement and wounding.

The earliest known representatives of the subfamily Capreolinae are from the Late Miocene sites Otovasca 1 (MN9, Moldova) and Răspopeni (MN10, Moldova), where *Procapreolus* sp. and

Cervavitus sp. were respectively identified (Lungu and Rzebik-Kowalska, 2011). A diverse group of primitive capreolines also originates from the Late Miocene of the Iberian Peninsula, represented by a small-sized deer with muntjac-like features ("Muntiacinae gen et sp. indet.") from the Late Miocene of Creventille-2 (Spain) (Croitor, 2021). While the cervid from Creventille-2 was as large as modern barking deer, it is characterized by relatively narrower and higher upper molars when compared to Asian muntjacs (Croitor et al., 2020). Deer from the genus *Lucentia* (*L. iberica* and *L. pierensis*) are somewhat larger, found in the Late Miocene of the Iberian Peninsula (MN11), but retain their primitive two-pointed antlers with a very high position of bifurcation (Azanza, 2000).

The next stage of capreoline evolution, characterized by three-pointed antlers, is represented by the genus *Procapreolus*, which underwent the most diversified evolutionary radiation among the early capreolines and dispersed as far as eastern regions of Eurasia (Croitor et al., 2020). The three-tined antlers with a high position of the first ramification and a distal more or less dichotomic fork represent the most common antler bauplan of Capreolinae, maintained, for instance, by modern *Capreolus*. This is the initial stage for practically all known diversity of antler shape in telemetacarpal deer, including the Old World genus Alces and the American Capreolinae.

The transition from the three-pointed antler condition of *Procapreolus* to a more specialized antler shape is represented by *Damacerus bessarabiae*, which acquired an additional morphologically variable distal tine. Despite the advanced specialization of antlers that evolved a small distal palmation, *D. bessarabiae* maintains primitive dental features, such as the unmolarized lower fourth premolar and the strong *Palaeomeryx* fold in lower molars.

The next stage of evolution is represented by *Metadicrocerus variabilis*, which maintained the basic three-pointed antler bauplan but evolved multiple tine bifurcations of its palmated antlers. It is important to mention that a similar way of evolving multi-tined palmated antlers is assumed for *Alces* (Bubenik, 1990).

The Pliocene deer from Udunga in the Trans-Baikal Area shows the typical shape of the Alces frontal bone, with lateral orientation of the pedicles, suggesting that the lineage of elks continued to evolve in the eastern part of the Eurasian continent after the mass extinction of telemetacarpal deer from Europe. Most likely, the origin of all elks is related to the cervid from Udunga. The elk from Udunga is characterized by an oblique position of the antler burr, as seen in *Alces gallicus*, and a slight anteroposterior compression of the pedicle. The oldest remains of *A. gallicus* are known from the Middle Villafranchian of Navrukho (Tajikistan) and Livenzovka (Azov Sea Area of Russia) (Vislobokova, 1986; Nikolsky and Titov, 2002). Azzaroli (1953), Heintz and Poplin (1980), Lister (1987), Breda and Marchetti (2005), and Nikolsky (2010) regard Eurasian fossil elks as chronospecies of a single phyletic lineage, characterized by a gradual increase in body size and a shortening of the antler beam. However, the elk species described from the Pleistocene of Europe probably do not belong to a successive phyletic lineage, but instead represent specialized side branches. This is the case with *A. gallicus*, which is characterized by extreme specialization of antler morphology with a very large antler span, caused by elongation of the basal segment of the antler. Therefore, the antlers of *A. gallicus* should be regarded as extremely specialized and distant from the initial capreoline antler bauplan. Some characters (*Palaeomeryx* fold, unmolarized P_3, long nasal bones) are still primitive, but the relatively short braincase suggests that we are dealing with a quite advanced elk form that most probably represents a side evolutionary branch that dispersed to Western Europe. The river meadows in the temperate open plains of Asia represent the most probable ecosystems where *A. gallicus* evolved. The unmolarized P_3 of *Cervalces* scotti may be regarded as evidence that this North American species, together with *A. gallicus*, is part of the first successful evolutionary radiation of elks, occurring before the process of P_3 molarization that occurred in *Alces latifrons*. The elongated braincase of *A. latifrons* rules out a direct phyletic relationship with European *A. gallicus* (Croitor, 2018b). One can assume that *A. latifrons* evolved in Asia and then substituted *A. gallicus* during the early Middle Pleistocene.

The origin of *Rangifer* is also related to the middle latitudes of Siberia. The discovery of a frontoparietal skull fragment of *Rangifer* sp. from the Early Pleistocene of Isakovka-4 (Omsk, Russia), dated back to 2.1-1.8 Ma, allows us to consider Northern Eurasia as a possible center of reindeer origin (Bondarev et al., 2017). The specimen from Isakovka-4 is characterized by the typical for reindeer shape of frontoparietal suture and the short and broad braincase, while the pedicles, unlike those of modern reindeer, are inclined backwards and set parallel to each other, demonstrating the primitive morphological condition of cervids. The associated fauna and flora indicate relatively warm climatic conditions (Bondarev et al., 2017).

All known Middle and Late Pleistocene reindeer of Eurasia share a peculiar specialized antler shape with the short distance between the first and second tines, similar to the advanced American barren-ground caribou. This led Geist (1998) to suggest that all reindeer from the Middle and Late Pleistocene of the Old World stem from this advanced North American form. According to Geist (1998), the first dispersal event of reindeer in Eurasia occurred during the Riss Glaciation.

The genetic difference between the tundra subspecies *Rangifer tarandus tarandus* and the forest subspecies *R. tarandus fennicus* is not as significant as that between the North American forest caribou and barren ground caribou. Mitochondrial DNA analysis shows that the modern Eurasian tundra and forest subspecies have a diphyletic origin from two distinct refugia. One refugium, located in western Eurasia, was in close proximity to the extensive ice sheet that covered Fennoscandia, and the other, larger refugium was situated in Beringia (Røed, 2005).

The paleontological record is consistent with genetic data. The fossil record shows that the origin of the reindeer with relatively small teeth, known as "*R. tarandus guettardi*," occurred in the smaller Western refugium, while the origin of *R. tarandus constantini* is related to the Beringian refugium. During the last glacial maximum, *R. tarandus constantini* dispersed westward and interbred with local European reindeer forms (Croitor, 2010).

According to Rankama and Ukkonen (2001), Western Europe is the probable area of origin of modern tundra reindeer. In contrast to fossil *Rangifer*, modern subspecies of Eurasian reindeer are specialized concentrate feeders, with small cheek teeth and reduced lower incisors and canines that do not participate in food gathering. They take forage by their lips and have an enlarged nasal cavity as an adaptation to breathing cold and dry air (Flerov, 1952; Sokolov, 1959). The specific adaptations of *R. tarandus fennicus* to forest habitats evolved after the post-glacial extension of forests and are considered secondary adaptations (Geist, 1998; Røed, 2005). Rankama and Ukkonen (2001) propose that the origin of forest reindeer may be related to the forested refugium in the East of Fennoscandia. This hypothesis is supported by Alekseeva's (1990) discovery of a fossil reindeer skull from Tatarstan (Russia) that resembles modern *R. tarandus fennicus*.

6.2. Dispersals and paleobiogeography of Cervinae in western Eurasia

The evolutionary radiation of the subfamily Cervinae is geographically compact, primarily located in the eastern part of the Oriental zoogeographic province, and remains relatively intact until the present day (Geist, 1998). Unlike the subfamily Capreolinae, which comprises a radiation of telemetacarpal deer in the temperate latitudes of western Eurasia, the subfamily Cervinae represents the evolutionary radiation that primarily occured in the tropical and subtropical latitudes of southeastern Asia. The eastern part of the Oriental zoogeographic province is the area of the highest diversification of the subfamily Cervinae and is considered the hypothetical center of the initial radiation of plesiometacarpal deer (Geist, 1998; Di Stefano and Petronio, 2002; Croitor, 2014).

An overview of Late Miocene cervids from western Eurasia reveals a notable absence of deer in the subfamily Cervinae. The first representatives of Cervinae appear in Early Pliocene faunas of Eastern Europe and belong to three different genera with varying degrees of evolutionary specialization: *Praeelaphus australorientalis*, *P. warthae*, *Metacervocerus pardinensis*, and *Rucervus* (*Arvernoceros*) *ardei* (Croitor, 1997; Croitor and Stefaniak, 2009). These species represent the first significant Late Miocene radiation of Cervinae, which today includes species such as *Axis axis* and *Rucervus duvaucelii* found in Southeast Asia (Pitra et al., 2004).

Rucervus was the longest-lived lineage of plesiometacarpal deer in western Eurasia. The earliest known record of *Rucervus* (*Arvernoceros*) *comes* from Weze-1, Poland, in the Early Pliocene (Croitor and Stefaniak, 2009). Remains of *R.* (*Arvernoceros*) *ardei* have been found in Late Pliocene deposits in France, Spain, and Moldova (Heintz, 1970; Croitor, 2009). The next evolutionary stage of this lineage is represented by *R. radulescui*, which was about the size of a red deer, and is known from Early Pleistocene deposits in Romania. Another species, *R. verestchagini*, which was about the size of a wapiti, is known from Early Pleistocene deposits in Moldova and Crimea (Croitor, 2018).

The *R.* (*Arvernoceros*) *lineage* survived in the Iberian glacial refugium as the specialized endemic form *Haploidoceros mediterraneus* until the Late Pleistocene. New data on antler morphology from remains of *H. mediterraneus* recovered from Cova del Rinoceront suggest that this species belongs to the *R.* (*Arvernoceros*) phylogenetic stock. This conclusion is based on the presence of vestigial or atavistic posterior crown tine in the antlered skull CR-6189, combined with cranial morphology that does not contradict such a phylogenetic relationship (Croitor et al., 2020). Dental morphology, shape of short pedicles, and the proximal portion of antlers confirm the probable direct phyletic relationship between *H. mediterraneus* and "*Cervus elaphoides*" from the Early Pleistocene site of Venta Micena. The small accessory prong situated on the first tine or in the area of basal ramification in "*Cervus elaphoides*" from Venta Micena confirms its affinity to modern *R. duvaucelii* and Early Villafranchian *R.* (*A.*) *ardei*. Unlike *R.* (*A.*) *ardei*, the cervid from Venta Micena is characterized by the absence of a cingulum in the upper molars and the frequent molarization of P_4. We agree with Lister's (1990) opinion that the small-sized cervid from Venta Micena is a genuine and yet undescribed species (Croitor et al., 2020).

The genus *Praeelaphus* is a phylogenetic lineage of plesiometacarpal deer that first appeared in the Early Pleistocene of Europe and had a long evolutionary history in the western Palearctic. *Praeelaphus* is represented by several forms in western Eurasia, distinguished by body size and some details in antler morphology. Deer of the genus *Praeelaphus* have primitive dental morphology. However, the length of the braincase in *Praeelaphus* is relatively short, while four-pointed antlers are rather specialized with flattened distal portions and other morphological details. The shape of the basioccipital in *Praeelaphus* suggests that this genus does not belong to the evolutionary stock of *Cervus elaphus* (Croitor, 2017). The two earliest species of the genus, *P. australorientalis* and *P. warthae*, represent two sister lineages of this genus in western Eurasia. Other species of the genus, including the better-known *P. perrieri* from the Late Pliocene of Western Europe, represent the local evolution of the warthae lineage. Like the deer of the *Arvernoceros* lineage, *Praeelaphus* was adapted to relatively warm climate conditions and became extinct in most parts of the western Palearctic during the first glacial pulses that marked the beginning of the Pleistocene (Croitor, 2017). The last representatives of the genus *Praeelaphus* survived in Pleistocene glacial refugia of western Eurasia, such as Transcaucasia (the Early Pleistocene of Dmanisi, Georgia) and the Italian Peninsula (the Early Pleistocene of Olivola, Tuscany). Most probably, the endemic dwarfed deer *Cervus* (*Euryceros*) *messinae* Pohlig, 1909 from the Middle Pleistocene of Sicily is the latest representative of *Praeelaphus* that survived in conditions of insular isolation. *Praeelaphus messinae* is characterized by a roe-deer-like body size and some features of antlers (the flattened area of antler ramification, the pyriform beam cross-section) characteristic of continental Praeelaphus.

Cervus nestii is a small cervid from the Early Pleistocene of Olivola and Upper Valdarno

(Italy) and Dmanisi (Georgia), representing the early radiation within the genus *Cervus sensu stricto* and the early dispersals of this genus in the Western Palearctic. This species already exhibits the typical modern red deer cranial morphology, including the elongated splanchnocranium (particularly its orbitofrontal portion), combined with the *'Muntiacus'*-like narrow triangular basioccipital. The frontal orientation of the distal antler fork is another specific character shared by *C. nestii* and the primitive subspecies of red deer, such as extinct *C. elaphus acoronatus* and modern *C. elaphus bactrianus*. However, unlike modern red deer, *C. nestii* lacks the bez tine and has a relatively small body size of about 60 kg.

C. elaphus, the red deer, spread across western Eurasia during the early Middle Pleistocene. The local evolution of *C. elaphus acoronatus* produced a wide variety of subspecies and forms during the Middle and Late Pleistocene, most probably resulting from the combination of several dispersal events from the east and local evolutionary processes in the western (the Iberian Peninsula) and eastern (the Italian Peninsula, Balkans, and Anatolia) glacial refugia.

The Italian Peninsula is of particular interest from a paleozoogeographic standpoint, as it had a broader connection with the Balkan Peninsula during glacial periods and acted as part of the Balkan-Italian glacial refugium. The geographic isolation of the Italian Peninsula during interglacial periods led to partial isolation of local red deer populations, which created conditions for the local evolution of such forms as *C. elaphus rianensis* and *C. elaphus aretinus*.

Wapiti, *Cervus canadensis*, appeared in the western Palearctic area during the Late Pleistocene in the context of periglacial fauna. *C. canadensis* and *C. elaphus* are vicariant species according to their ecological requirements and biogeographic distribution. The Western Palearctic wapiti persisted into the Holocene in the refugia of the Scandinavian Peninsula and the Alpine area. Episodic climate cooling during the Younger Dryas prolonged the existence of *C. canadensis* in the European fauna. The Alpine population of wapiti evolved into a specialized form with palmated antlers, *C. canadensis palmidactyloceros*, which dispersed into the Italian Peninsula, as well as colonized the Island of Capri, where it evolved into an endemic dwarfed insular form, *C. canadensis tyrrhenicus*.

Traditionally, the tribe Megalocerotini *sensu lato* (Vislobokova, 1990, 2013) was believed to be a genuine monophyletic group. However, this tribe is, in fact, polyphyletic in nature. The cervid forms grouped under the term "giant deer" or "large-sized deer" actually represent several lineages that evolved similar convergent adaptations (the large body size, the large and complicated palmated antlers) in similar conditions (open landscapes of temperate latitudes). The mandibular and cranial pachyostosis reported as an important diagnostic character of megacerines (Vislobokova, 1990; 2009; 2012; 2013) is a secondary metabolic response to exogenic factors, primarily the marked seasonality (Lister, 1994; Croitor, 2016). All known pachyostotic cervids belong to the subfamily Cervinae and evolved and lived in the most peripheral and extreme parts of the distribution area of this subfamily (Croitor, 2016). This is the case with *M. giganteus* which had a distribution in the cold middle latitudes of Eurasia with strong seasonality. *Sinomegaceros pachyosteus* is another pachyostotic cervine species that may have been affected by the repeatedly advancing arid zones of Central Asia.

The tribe Megalocerotini Brookes, 1828 sensu stricto includes the genera *Megaloceros*, *Megaceroides*, *Praedama*, and *Dama*, which represent a monophyletic phylogenetic branch that radiated in the western part of the Palearctic. However, the present state of knowledge does not provide a satisfactory diagnosis for this restricted group of genera that contain extremely specialized forms.

Multivariate cluster analysis of antler characters and pachyostosis development reveals that *Megaloceros giganteus* is closely related to *Dama dama*, and both species are associated with the genera *Rucerus* and *Cervus* (Fig. 4). In contrast to the widely accepted opinion that *Praesinomegaceros*, *Sinomegaceros*, *Megaloceros*, and *Rucervus* (*Arvernoceros*) *represent* a natural systematic group of Megacerini (Vislobokova, 1990, 2012; van der Made and Tong, 2008), the multivariate analysis shows that the *Praesinomegaceros* / *Sinomegaceros* lineage is morphologically quite distant from *Megaloceros* and *Rucervus* (*Arvernoceros*).

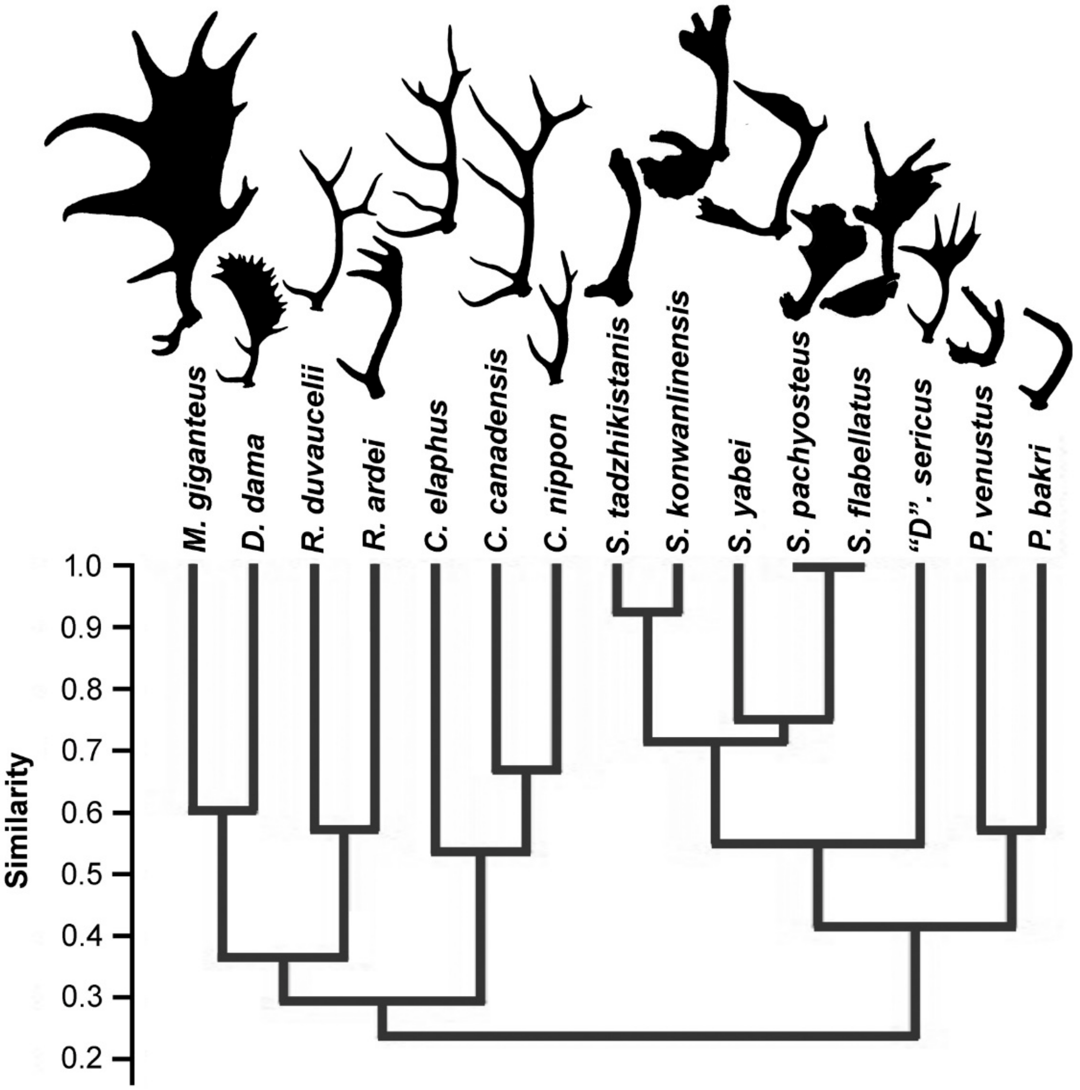

Fig. 4. Cluster analysis of the diagnostic antler characters combined with pachyostosis development of large-sized deer (*Megaloceros*, *Sinomegaceros*) and selected modern and extinct deer species. The cophenetic correlation is 0.8481

The results also indicate that the cranial pachyostosis that evolved in *Megaloceros* and *Sinomegaceros* represents physiological evolutionary parallelism and does not have a taxonomical value above the genus level (Croitor, 2016). *M. giganteus antecedens*, the earliest form of giant deer in Europe that shows adaptations to the wooded biome, is most likely a side specialized branch of the giant deer lineage. The apparent "*Sinomegaceros*"-like antler shape of *M. giganteus antecedens* resulted from significant shortening of antlers that caused the coalescence of the middle and posterior tines with the distal palmation (Croitor, 2021).

Analysis of antler morphology confirms the close relationship between *Megaloceros* and *Dama*, as demonstrated by a recent paleogenetic study (Lister et al., 2005), and supports the relationship between *Rucervus* (*Arvernoceros*) ardei and *Rucervus duvaucelii* (Croitor, 2018).

The phylogenetic branch of *Megaloceros-Praedama-Dama* is probably related to the genus

Metacervocerus, which dispersed from Southeast Asia to Europe during the Early Pliocene (Croitor, 2021). *Metacervocerus* had several species with simple three-tined antlers, similar to those found in modern *Axis axis*, during the Pliocene and Early Pleistocene of Eurasia. Certain representatives of the genus, such as *M. pardinensis* and *M. punjabiensis*, exhibit specific features (cingulum in upper molars and relatively long braincase, respectively) that are also found in *Megaloceros*.

The core area of giant deer evolution and geographic distribution is related to the open wooded habitats of southwestern Siberia and northern Kazakhstan, where the *Megaloceros* phylogenetic branch originated. *Praedama* is a side evolutionary branch of the *Megaloceros* lineage, which dispersed in Europe by the end of the Villafranchian. Early representatives of *Praedama* already possessed the typical antler structure of *Megaloceros*, along with a weak development of mandibular pachyostosis. *Praedama giulii* (Kahlke, 1997) from the late Early Pleistocene of Germany is a specialized large cursorial deer with very long metapodials. This evolutionary specialization was maintained in most Eurasian giant deer forms.

M. giganteus repeatedly dispersed into Western Europe following Pleistocene climate fluctuations and gave rise to forest and woodland forms, such as *M. giganteus antecedens*, *M. giganteus ruffii*, and *M. giganteus megaceros*. The advancing glaciations triggered geographic isolations, southward dispersals, and local endemic evolutionary processes that gave rise to specialized forms, such as *M. giganteus padanus* (Vialli, 1939) from the Late Pleistocene of Italy, *M. mugharensis* (di Stefano, 1996) from the Middle Pleistocene of the Near East, and *Megaceroides algericus* (Lydekker, 1890) from the Late Pleistocene to early Holocene of North Africa. Therefore, *Megaloceros* is one of the few cervids that colonized North Africa, possibly due to its physiological capacity to tolerate brief seasonal food shortages (Croitor, 2016). The extraordinary adaptability of the antlers of giant deer contradicts the dominated in literature assumption that they were a harmful overspecialization leading to the extinction of *M. giganteus*.

The genus *Praemegaceros* represents another group of large-sized deer that evolved some morphological features convergent with those of *Megaloceros*. The oldest known species of *Praemegaceros* is *P. obscurus*, which dates back to 1.81 Ma and was found in Dmanisi, suggesting a South Asian origin for this species. The origin of *P. obscurus* can be traced through the paleontological record of the Sivalik Hills. Most of the antler characters of *Panolia* sp. from the Siwalik Hills (such as the strong basal tine, the strong backward bending of the beam, and the obtuse angle of the first ramification) correspond to the antler morphology of *P. obscurus*. The accessory prongs in the area of the first ramification are also common for modern *Panolia eldii* and recall the position of the dorsal tine in *Praemegaceros obscurus*. Therefore, one can assume that *P. obscurus* is a large-sized descendant of *Panolia* sp. from the Siwaliks. The suggested phylogenetic relationship between *Eucladoceros* and *P. obscurus*, made by Radulesco and Samson (1967) and Azzaroli and Mazza (1992b, 1993), is correct, as both genera are closely related to modern cervid forms of the *Cervus* phylogenetic stock. However, the character of this phylogenetic relationship is more complicated. *Praemegaceros pliotarandoides* and *P. verticornis* are also closely related to *P. obscurus*, but they are more morphologically distant from *Panolia eldii*.

The origin of the Cretan endemic genus *Candiacervus* is linked to the continental genus *Praemegaceros*. The genus *Candiacervus* comprises several dwarfed insular species that exhibit varying degrees of antler simplification and specialization (van der Geer, 2018). The less specialized species, *Candiacervus devosi* van der Geer, 2018, is characterized by a recognizable antler bauplan and the presence of all structural elements (including the dorsal tine, middle tine, and posterior tine), indicating a direct evolutionary relationship with a continental *Praemegaceros* species (*P. obscurus* or *P. verticornis*).

CONCLUSIONS AND RECOMMENDATIONS

A taxonomic survey of Late Miocene to Late Pleistocene fossil deer from the Western Palearctic area established the presence of 27 genera and 78 species in this biogeographic zone. The main characteristics of the taxonomic diversity of fossil deer from the studied area are the following:

1) Late Miocene cervids of Western Eurasia belong to the early evolutionary radiation of the subfamily Capreolinae. This radiation of archaic capreolines includes a wide variety of forms, exhibiting different levels of evolutionary specialization. The diversity of archaic capreolines is generally comparable to the diversity of the subfamily Cervinae, which we observe today in Southeast Asia. The holometacarpal deer from the Late Miocene of Europe are the archaic representatives of the subfamily Capreolinae. Based on the results obtained, the subfamily name Pliocervinae is a junior synonym of the subfamily Capreolinae. The genera *Lucentia*, *Turiacemas*, *Pliocervus*, *Damacerus*, *Metadicrocerus*, and *Pavlodaria* are all included in the subfamily Capreolinae. Some of the morphological features that characterize the early evolutionary radiation of capreolines include the rather conservative general roe-deer-like plan of antler construction, the relatively long series of premolars, the advanced molarization of the lower P_4 premolar, and the *Palaeomeryx* fold on the lower molars.

2) The genus *Cervavitus*, previously used to denote the transitional evolutionary stage between primitive deer and modern cervines, has been found to be polyphyletic and artificial. Nomenclatural analysis indicates that *Cervavitus* is a junior synonym of *Damacerus*, which is recommended for use in this work. The European cervid forms previously included in the genus *Cervavitus* (*Damacerus bessarabiae* Khomenko, 1913, and *Metadicrocerus variabilis* [Khomenko, 1913]) belong to the early evolutionary radiation of the Capreolinae subfamily. The early evolutionary stage of the telemetacarpal morphological state characteristic of capreolines is represented by *M. variabilis* from the Late Miocene of Ukraine. However, the cervid forms from Asia included in the genus *Cervavitus* do not belong to the subfamily Capreolinae and require taxonomic and systematic revision.

3) The subfamily name Pliocervinae, as proposed by Symeonidis in 1974, has been identified as a junior synonym of the subfamily Capreolinae Brookes, 1828. Consequently, if the tribe Pliocervini is to be retained, it should be included in the subfamily Capreolinae and limited to the genera *Pliocervus* and *Pavlodaria*.

4) The majority of the archaic members of the Capreolinae subfamily disappeared prior to the Pliocene epoch. The surviving lineages, represented today by the genera *Alces*, *Rangifer*, *Capreolus*, and *Hydropotes*, are the result of early capreoline dispersals to East Asia and subsequent local evolutionary processes. As such, the evolution of the modern Eurasian capreoline genera is

closely linked to the eastern Palearctic zone.

5) The subfamily Cervinae first dispersed into western Eurasia during the early Pliocene, with the earliest European representatives being related to the modern genera *Axis* and *Rucervus* from the Eastern Biogeographic Realm. This dispersal event was significant in shaping the modern zoogeographical distribution of cervid subfamilies in Eurasia. During the Pleistocene, repeated dispersals of the subfamily Cervinae from eastern Eurasia, in combination with glacial/interglacial cycles, led to multiple local evolutionary processes in the glacial refugia of the southern part of Western Palearctic, where endemic species and genera of deer evolved. *Haploidoceros mediterraneus* from the Middle Pleistocene of Southeast France and the Upper Pleistocene of the Iberian Peninsula, as well as *Megaceroides algericus* from the Upper Pleistocene of North Africa, are continental endemic species that attained the highest degree of evolutionary specialization among Palearctic representatives of the subfamily Cervinae. The taxonomic diversity of the family Cervidae reached its highest level during the early and middle Pleistocene.

6) Deer antlers have evolved primarily for intraspecific communication of males during the rutting period, such as fighting or demonstrating hierarchical position. However, antler evolution is influenced by multiple factors that can directly or indirectly affect the shape and communication function of antlers. Protection and security are also important antler functions in Palearctic cervids, leading to their specific and complex construction, which has evolved multiple times in different lineages. The increased body size of Palearctic deer comes with a higher risk of fatal wounds during male fights. However, this negative effect is compensated by the development of additional tines and antler bifurcations that provide protection. The basal (eye or brow) tine is often doubled, bifurcated or flattened in Palearctic deer, and serves as the first level of protection for the head and eyes. The middle (trez) tine, which has the function of locking with the antlers of a rival, is specific to deer from high latitudes and never appears in tropical species. The posterior tine has evolved independently in several Palearctic lineages adapted to open landscapes, serving as a scratch grooming adaptation against ectoparasites that weaken male health and decrease vigilance during the rutting period.

7) Small-sized deer with "*Dama*-like" characteristics, often classified under the genus *Pseudodama* Azzaroli, 1992, actually belong to different phylogenetic lineages and various modern and extinct genera, such as *Cervus*, *Dama*, *Metacervocerus*, and *Praeelaphus*. The genus name *Pseudodama* should be restricted to its type species *Dama nestii nestii* and considered a junior synonym of the genus *Cervus*.

8) Small and relatively primitive representatives of the modern genera *Cervus* (*Cervus nestii*) and *Dama* (*Dama eurygonos*) first appeared in the Western Palearctic during the Early Pleistocene.

9) The close phylogenetic relationship between *Megaloceros*, *Dama*, and *Praedama* is

supported by the multivariate analysis of craniodental diagnostic characters. However, the presumed relationship between *Megaloceros* and *Sinomegaceros* is not confirmed by the cluster analysis of antler morphology.

10) The tribe Megalocerotini Brookes, 1828 (= Megacerini Viret, 1961) *sensu lato* is polyphyletic, comprising cervid forms belonging to three distinct phylogenetic branches. The first branch includes *Rucervus* (*Arvernoceros*) *ardei*, which is part of the early evolutionary radiation of Cervinae. The second branch includes *Megaloceros*, *Megaceroides*, *Praedama*, and *Dama*, forming a phylogenetic radiation that occurred in the western part of Eurasia (*Megalocerotini sensu stricto*). Finally, the genus *Praemegaceros* belongs to the *Panolia eldii - Cervus elaphus* phylogenetic branch.

11) The extinction of most Pleistocene species in the subfamily Cervinae in the Western Palearctic zone can often be attributed to the ecological opportunism that defines the general ecological and evolutionary strategy of the family Cervidae. This strategy is highly advantageous for the colonization of new and unstable ecosystems that arise due to climate change. However, ecologically opportunistic species can be vulnerable in the face of strong ecological competition with herbivores that have evolved a higher degree of ecological and evolutionary specialization, including other members of the family Cervidae.

12) The endemic forms of fossil deer from the Mediterranean islands have diverse systematic origins, and in some cases, morphological data allow us to establish their phylogenetic relationships with continental species. Thus, *Praemegaceros cazioti* from the Upper Pleistocene of Corsica and Sardinia is phylogenetically related to *P. solilhacus* from the Middle Pleistocene, both of which are placed in the subgenus *Nesoleipoceros* Rădulescu and Samson, 1967. *Candiacervus devosi* from the Pleistocene of Crete shows morphological features in its antlers that suggest a direct phylogenetic relationship with *Praemegaceros obscurus* or *P. verticornis* from the Early and Middle Pleistocene of Europe, respectively. *Cervus* (*Euryceros*) *messinae* from the Middle Pleistocene of Sicily is most likely related to *Praeelaphus lyra* from the Pliocene of Italy.

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ANNOTATION

CROITOR Roman "Deer from Late Miocene to Pleistocene of the Western Palearctic: systematics, phylogeny and evolution". Thesis of doctor habilitate in biological sciences, Chisinau, 2023.

Thesis structure: introduction, six chapters, general conclusions and recommendations,. The main text spans 210 pages and is supported by 458 bibliographic sources, 2 annexes, 45 figures, 7 tables. The obtained results have been published in 70 scientific works.

Keywords: mammals, deer, Late Miocene, Pliocene, Pleistocene, taxonomy, systematics, evolution, phylogeny, paleobiogeography.

Aim: Revise the taxonomy of fossil deer from the Late Miocene to the Late Pleistocene in the Western Palearctic to uncover phylogenetic relationships between fossil and modern cervids, explore their evolutionary and ecological diversification.

Research target interests: revision of taxonomy, systematics, phylogeny and evolution of fossil deer during the geological epoch from the Late Miocene to the end of the Pleistocene in the western Palaearctic; the taxonomic study based on revision of type material and the analysis of individual and evolutionary variability of cervids that permitted the verification of diagnoses of species and genera, the study of phylogenetic relationships of cervids, the identification of cervid evolutionary mechanisms, and the revealing of paleobiogeographic scenarios explaining the diversity of fossil cervids of western Palearctic in the past.

Scientific novelty and originality: the thesis proposes the first comprehensive taxonomic revision of fossil deer from Late Miocene to Late Pleistocene from western Palearctic zone based on the direct study of fossil material from the almost entire area of the western Palearctic (23 paleontological collections from 12 countries). Two genera, three species, and one subspecies described by the author. The study proposes the new phylogenetic model of crown deer (subfamilies Cervinae and Capreolinae) that reveals the phylogenetic relationships of fossil deer with previously uncertain phylogenetic position. The study for the first time applied evaluation of taxonomic significance of craniodental characters in cervids using the molecular genetic data and applied the obtained data in supervised hierarchical clustering in order to find the systematic position of fossil species among modern cervids.

The main results obtained: The work includes taxonomic study of 27 genera and 78 species and forms of fossil deer. The new phylogenetic model of crown deer of the family Cervidae is proposed. The systematic position and evolutionary significance of some previously poorly known species and taxonomic groups of higher grade are revealed; the phylogenetic relationships between modern deer and extinct forms are demonstrated; the mechanisms and principles of deer evolution and diversification are described. Two new genera and three new species, as well as one subspecies of fossil deer are described. Also, other potentially new taxa at genus and species level are indicated.

Theoretical significance: the proposed comprehensive model of the evolution and phylogenetic relationships of the deer family in the western Palaearctic during the last ca. 10 million years fills the gaps in taxonomy and systematics between fossil and modern deer, explain their evlutionary ratiation in paleobiogeographic context.

The application value: The obtained results confirmed by the 70 high-quality scientific publications, explain the biodiversity and zoogeographic distribution of modern deer, reir responces to the climate change, the evolutionary history of endangered species that allow to build correctly the strategy of deer biodiversity protection.

Implementation of scientific results: the deer family is recommended as a reliable proxy for biostratigraphic and geochronological studies, as well as paleobiogeographic and paleoecological reconstructions. The results also allow us to evaluate the scientific, cultural and educational significance of the paleontological collections of the Republic of Moldova, as well as of the natural history collections from other countries of the European continent.

ADNOTARE

CROITOR Roman „Cerbii din Miocenul Târziu - Pleistocenul Palearcticului de Vest: sistematică, filogenie și evoluție", teză de doctor habilitat în științe biologice, Chișinău, 2022.

Structura tezei: introducere, șase capitole, concluzii generale și recomandări, bibliografia din 458 de titluri, 2 anexe, 210 de pagini de text de bază, 45 de figuri, 7 tabele. Rezultatele obținute sunt publicate în 70 de lucrări științifice.

Cuvintele-cheie: Mammalia, Cervidae, Miocen târziu, Pliocen, Pleistocen, taxonomie, sistematică, evoluție, filogenie, paleobiogeografie.

Scopul lucrării: Revizuirea taxonomică ale cerbilor din Miocenul Târziu până în Pleistocenul Târziu în Palaearcticul de vest pentru a dezvălui relațiile filogenetice dintre reprezentanții fosili și moderni ai familiei Cervidae, explorarea diversificării lor evolutive și paleoecologice.

Obiectivele cercetării: revizuirea taxonomiei, sistematicii, filogeniei și evoluției cerbilor fosili în perioada geologică cuprinsă între Miocenul Târziu și sfârșitul Pleistocenului în regiunea Palaearctică de vest; studiul taxonomic bazat pe revizuirea materialelor tip și analiza variației individuale și evolutive a cervidelor, care a permis verificarea diagnosticelor speciilor și genurilor, studiul relațiilor filogenetice ale cervidelor, identificarea mecanismelor evolutive ale cervidelor și dezvăluirea scenariilor paleobiogeografice care explică diversitatea cervidelor fosile din Palaearcticul de vest în trecut..

Noutatea științifică și originalitatea lucrării: Teza propune prima revizuire taxonomică exhaustivă a cerbilor fosili din Miocenul Târziu până în Pleistocenul Târziu din zona Palaearctică de vest, bazată pe studiul direct al materialului fosil din aproape întreaga zonă a Palaearcticului de vest (23 de colecții paleontologice din 12 țări). Sunt descrise două genuri, trei specii și o subspecie. Studiul propune un nou model filogenetic pentru cerbii de tip modern (Cervinae și Capreolinae), care dezvăluie relațiile filogenetice ale cerbilor fosili cu poziția filogenetică anterior incertă. Pentru prima dată, studiul a aplicat evaluarea semnificației taxonomice a caracterelor craniodentale la cervide folosind datele genetice moleculare și a aplicat datele obținute în clusterizarea ierarhică supervizată pentru a găsi poziția sistematică a speciilor fosile printre cervidele moderne.

Rezultate principiale: Lucrarea include un studiu taxonomic al 27 de genuri și 78 de specii și forme de cerbi fosili. Este propus noul model filogenetic al cerbilor de tip modern din familia Cervidae. Este dezvăluită poziția sistematică și semnificația evolutivă a unor specii și grupuri taxonomice de grad înalt anterior puțin cunoscute; sunt demonstrate relațiile filogenetice dintre cerbii moderni și formele fosile; sunt descrise mecanismele și principiile evoluției și diversificării taxonomice ale cerbilor. Sunt descrise două genuri noi și trei specii noi, precum și o subspecie de cerbi fosili. De asemenea, sunt indicate și alte taxoane potențial noi la nivel de gen și specie.

Semnificație teoretică: modelul comprehensiv propus al evoluției și relațiilor filogenetice ale familiei cerbilor în Palaearcticul de vest, în ultimii aproximativ 10 milioane de ani, completează lacunele în taxonomie și sistematică dintre cerbii fosili și cei moderni, explicând diversificarea lor evolutivă în contextul paleobiogeografic.

Valoarea aplicativă: rezultatele obținute, confirmate de cele 70 de publicații științifice de înaltă calitate, explică biodiversitatea și distribuția zoogeografică a cerbilor moderni, răspunsurile lor la schimbările climatice, istoria evolutivă a speciilor în pericol de dispariție, ceea ce permite construirea corectă a strategiei de protecție a biodiversității cerbilor.

Implementarea rezultatelor științifice: Implementarea rezultatelor științifice: familia cerbilor este recomandată ca o resursă solidă pentru studiile biostratigrafice și geocronologice, precum și pentru reconstrucțiile paleobiogeografice și paleoecologice.. Rezultatele ne permit, de asemenea, să evaluăm importanța științifică, culturală și educațională a colecțiilor paleontologice din Republica Moldova, precum și a colecțiilor de istorie naturală din alte țări ale continentului european.

АННОТАЦИЯ

КРОЙТОР Роман «Олени от позднего миоцена до плейстоцена запада палеарктики: систематика, филогения и эволюция», лиссертация доктора хабилитата, Кишинёв, 2022.

Структура диссертации: введение, 6 глав, общие выводы и рекоммендации, библиография включающая 458 источников, 2 приложения, 210 страниц основного текста, 45 иллюстраций, 7 таблиц. Полученные результаты опубликованы в 70 научных работах..

Ключевые слова: млекопитающие, олени, поздний миоцен, плиоцен, плейстоцен, таксономия, систематика, эволюция, филогения, палеобиогеография.

Цель работы: таксономия ископаемых оленей с позднего миоцена по поздний плейстоцен западной палеарктики с целью раскрыть филогенетические связи между ископаемыми и современными оленями, их эволюционное и экологическое разнообразие.

Задачи: пересмотр таксономии, систематики, филогении и эволюции ископаемых оленей с позднего миоцена до конца плейстоцена западной палеарктики; таксономическое исследование на основе пересмотра типового материала и анализа индивидуальной и эволюционной изменчивости оленей, с целью уточнить диагнозы видов и родов, изучить филогенетические отношения оленей, выявить механизмы их эволюции и раскрывать палеобиогеографические сценарии, объясняющие разнообразие ископаемых оленей западной палеарктики в прошлом..

Научная новизна и оригинальность: в данной диссертации впервые предлагается глубокий пересмотр таксономии ископаемых оленей с позднего миоцена по поздний плейстоцен западной палеарктики на основе прямого изучения ископаемого материала практически со всей территории западной палеарктики (23 палеонтологические коллекции из 12 стран). Автором были описаны два рода, три вида и одна подвид. Исследование предлагает новую филогенетическую модель оленей, раскрывющую филогенетические связи ископаемых форм с неясным систематическим положением. Впервые была применена оценка таксономической значимости краниодентальных признаков с привлечением молекулярно-генетических данных. Отобранные признаки были использованы для определения положения ископаемых видов среди современных оленей.

Основные результаты: проведено таксономическое исследование 27 родов и 78 видов и форм ископаемых оленей. Предложена новая филогенетическая модель семейства оленевых. Раскрыто систематическое положение и эволюционное значение некоторых ранее малоизученных видов и таксономических групп высшего ранга; раскрыты филогенетические связи между современными оленями и вымершими формами; описываются механизмы и принципы эволюции и разнообразия оленей. Описаны два новых рода и три новых вида, а также один подвид ископаемых оленей. Кроме того, указаны другие потенциально новые таксоны на уровне рода и вида..

Теоретическое значение: предложенная эволюционная и филогенетическпя модель ископаемых оленей западной палеарктики за последние приблизительно 10 миллионов лет заполняет пробелы в таксономии и систематике между ископаемыми и современными оленями, объясняя их эволюционное разнообразие в палеобиогеографическом контексте.

Прикладная значимость: полученные результаты, подтвержденные 70 научными публикациями, объясняют биоразнообразие и географическое распространение современных оленей, влияние изменения климата и эволюционную историю вымирающих видов, что позволяет разработать правильную стратегию охраны биоразнообразия оленей.

Внедрение научных результатов: олени рекомендуется в качестве надежного индикатора для биостратиграфических исследований, а также для реконструкций палеобиогеографических и палеоэкологических процессов. Результаты позволяют оценить научную, культурнр-образовательную значимость палеонтологических коллекций стран европейского континента.

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CROITOR ROMAN

CERBII DIN MIOCENUL TÂRZIU - PLEISTOCENUL PALEARCTICULUI DE VEST: SISTEMATICĂ, FILOGENIE ŞI EVOLUŢIE

Rezumatul tezei de doctor habilitat în științe biologice

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