MINISTRY OF EDUCATION AND RESEARCH
OF THE REPUBLIC OF MOLDOVA
INSTITUTE OF ZOOLOGY

Manuscript rights
C.Z.U:
569.734/736:62/63(043.2)

CROITOR ROMAN

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

165.02 ZOOLOGY

Doctor habilitatus thesis in biological sciences

Scientific consultants:	Toderaș Ion, Doctor habilitat University Professor, Academician, Zoology
	Brugal Jean-Philippe, Dr. HDr. DR Emérite CNRS Dir-adj. Recherche Institut Arkaia, Geology

Author:

CHISINAU, 2023

MIINISTERUL EDUCAȚIEI ȘI CERCETĂRII
REPUBLICII MOLDOVA
INSTITUTUL DE ZOOLOGIE

Cu titlu de manuscris
C.Z.U:
569.734/736:62/63(043.2)

CROITOR ROMAN

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

165.02 ZOOLOGIE

Teză de doctor habilitat în zoologie

Consultanți ştiinţifici:

Toderaș, Ion, doctor habilitat,
Academician, profesor universitar,
zoologie

Brugal, Jean-Philippe, Dr.,
HDr. DR Emérite CNRS Dir-adj.
Recherche Institut Arkaia,
geologie

Autorul:

CHIȘINĂU, 2023

CONTENT

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

2. METHODOLOGICAL APPROACH TO THE STUDY OF CERVID SYSTEMATICS AND PHYLOGENY

3. SYSTEMATIC DIVERSITY OF TELEMETACARPAL DEER (SUBFAMILY CAPREOLINAE BROOKES, 1828) IN WESTERN PALEARCTIC

4. SYSTEMATIC DIVERSITY OF PLESIOMETACARPAL DEER (SUBFAMILY CERVINAE GOLDFUSS, 1820) IN WESTERN PALEARCTIC

5. MAIN EVOLUTIONARY FEATURES OF CROWN CERVIDS FROM WESTERN PALEARCTIC

6. PALEOBIOGEOGRAPHY OF DEER FROM WESTERN PALEARCTIC

APPENDICES

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.

List of tables

List of figures

Fig. 4.3. 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

Fig. 4.4. 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

Fig. A.1. The holotype skull of *Procapreolus moldavicus* (Janovskaya, 1957) from Lebedenco (= Fagadil), Cahul district, Moldova

Fig. A.2. *Procapreolus moldavicus* (Janovskaya, 1954): the male skull Nr. 220 (IZW) from Węże-1 (Poland); A, the frontal view; B, the palatal view of rostral part (the alveolus of the upper canine is indicated by the arrow); C, the side view

Fig. A.3. The isolated M^{1-2} (Nr. 77, IZC) of *Procapreolus moldavicus* (Janovskaya, 1954) from Tatareşti, Moldova

Fig. A.4. A, the holotype of *Procapreolus vesti* Korotkevich, 1970 (adapted from Korotkevich 1970); the neotype of *Procapreolus cusanus* (Croizet & Jobert, 1928) (adapted from Heintz 1970).

Fig. A.5. *Procapreolus cusanus* (Croizet & Jobert, 1828) from Ravine Les Etouaires (Issoire, France): the left ramus of mandible Nr. 5237, MNHN ("Collection of Croizet"). A, the occlusion view of lower tooth row; B, the lateral view of mandible

Fig. A.6. Antler fragments of *Pliocervus matheroni* (Gervais, 1852) from Cucuron, France: A, left antler LUB-783 (anterior view) with transversal cross-sections; B, fragment of left ramification with transversal cross-sections; C, LUB-782 (anterior view); D, LUB-782 (medial view); E, LUB-784 (anterior view)

Fig. A.7. Dental morphology of *Pliocervus matheroni* (Gervais, 1852) from Cucuron: A, occlusion view of the upper right incomplete tooth tow (P^2, P^4-M^3) LUB-798; B, occlusion view of lower fourth premolar (P_4) LUB-812; *prtf*, protoconal fold; *etst*, entostyle; *mtcf*, metaconule fold; *mtcd*, metaconid; *trgv*, trigonid valley; *prcd*, paraconid

Fig. A.8. The antlered skull of *Damacerus bessarabiae* Khomenko, 1913 from Cimişlia (no number, PMUB): A, Right- side oblique view with transversal antler cross- sections; B, frontal view of skull; *ofrd.*, orbito- frontal ridge

Fig. A.9. Antlered skull Nr. 43-1612 of *Metadicrocerus variabilis* (Aleksejev, 1913) from the Late Miocene of Novoelizavetovka, Ukraine: A, side view; B, frontal view

Fig. A.10. The antlered skull Nr. 1923-4 (MNHN) of *Croizetoceros ramosus* (Croizet & Jobert, 1828) from Sénèze

Fig. A.11. The left ramus of the mandible Nr. 3286/5 (SMNH) of *Alces sp.* from Mosbach (Germany). A, the side view of the mandible; B, the occlusion surface of the tooth row. Note the complete fusion of the metaconid and paraconid in P_3

Fig. A.12. The right antler of *Rangifer tarandus tournalii* (De Serres, 1829), holotype

Fig. A.13. *Praemuntiacus pidoplitschkoi* (Korotkevich, 1964): the left antler with pedicle from the Kuchurgan Gravel, Ukraine: A, the median view; B, the anterior view (adapted from Kototkevich, 1965)

Fig. A.14. The neotype of *Metacervocerus pardinensis* (Croizet & Jobert, 1828) from Perrier-Etouaires, France (MNHN, Paris): A, the lateral view; B, the median view

Fig. A.15. The antlered male skull CEY-2-2318 (Museum of Prehistory of Les Eyzies-de-Tayac) of *Metacervocerus rhenanus* (Dubois, 1904) from Ceyssaguet, France

Fig. A.16. The female skull of *Metacervocerus rhenanus* (Dubois, 1904) Nr. 210638 (PMUL) from Sénèze, France

Fig. A.17. The holotype Nr. 1 (IZW) of *Praeelaphus warthae* (Czyżewska, 1968) from Węże-1, Poland: A, the side view; B, the occlusion view of right cheek tooth row

Fig. A.18. The holotype OF24995 (NMENH) of *Praeelaphus australorienalis* Croitor, 2017 from Velikoploskoe (Ukraine): A, side view; B, occipital view

Fig. A.19. The antlered braincase IGF1378 of *Praeelaphus* from Olivola, Italy: A, side view; B, anterior view of the distal part of left antler; C, upper view of the occipital profile; D, posterior view of the braincase; E, basioccipitale view of the braincase

Fig. A.20. The left antler of *Praeelaphus messinae* (Pohlig, 1909) from the Pleistocene deposits of the Puntali cave (Sicily): A, medial view; B, lateral view

Fig. A.21. The right shed antler of *Rucervus* (*Arvernoceros*) *ardei* Croizet et Jobert, 1828 from Slobozia Mare (the Museum of Slobozia Mare, Cahul District, Moldova): A, lateral view; B, anterior view

Fig. A.22. *Rucervus radulescui* sp. nov. from Valea Grăunceanului: holotype, the left shed antler "GR-965, c. 17, v. 690" (Institute of Speleology "Emil Racoviță"; ISER): (A) medial view; and, (B) basal view

Fig. A.23. *Rucervus gigans* Croitor, 2018 from Apollonia-1: the lateral view of the left mandibular ramus APL-384 (syntype; School of Geology of the University of Thessaloniki, SGUT) and the shape of the occlusal surface of toothrow

Fig. A.24. *Rucervus gigans* Croitor, 2018 from Apollonia-1: the left maxilla APL-274 (syntype; SGUT) with tooth series P^2-M^3: grinding surface view

Fig. A.25. *Rucervus gigans* Croitor, 2018 from Apollonia-1: the basal fragment of antler APL-357 (syntype, SGUT)

Fig. A.26. The lectotype LV-I-9-1179 of *Haploideceros mediterraneaus* (Bonifay, 1967) from Lunel-Viel (France)

Fig. A.27. The antlered skull of *Haploideceros mediterraneaus* (Bonifay, 1967) from Cova del Rinoceront (Spain)

Fig. A.28. Lower mandible and lower cheek tooth rows of *Haploideceros mediterraneaus* (Bonifay, 1967) from Cova del Rinoceront (Spain)

Fig. A.29. Antler shape of (A) *Sinomegaceros insolitus* (Vekua et al., 2010) from the Early Pleistocene of Dmanisi (Georgia) and (B) *Sinomegaceros pachyosteus* from the Middle Pleistocene of northern China (adapted from Teilhard de Chardin and Pei 1941)

Fig. A.30. The partially preserved skull of *Eucladoceros dicranios* (Nestii, 1841) from Upper Valdarno, Italy (stored in the University of Florence): A, side view; B, cross-section of the antler below the basal ramification; C, occlusion view of the upper cheek tooth row

Fig. A.31. The antler shape of various forms of *Eucladoceros* from the western Palearctic: A, *E. ctenoides ctenoides* (Nesti, 1841) from Upper Valdarno, Italy (IGF377, MGUF); B, *E. ctenoides falconeri* (Dawkins, 1868) from Sénèze, France (MNHN); C, *E. ctenoides olivolanus* (Azzaroli and Mazza, 1992) from Olivola (IGF1402, MGUF); D, *E. ctenoides tetraceros* (Dawkins, 1878) from Peyrolles, France (34409, NHML); E, *E. dicranios* (Nesti, 1841) from Upper Valdarno, Italy (IGF270, MGUF); F, *E.* aff. *boulei* Teilhard de Chardin & Piveteau 1930 from Kapetanios, Greece

Fig. A.32. The skull of *Eucladoceros ctenoides falconeri* (= *Eucladoceros senezensis*) from Seneze. The specimen is in the paleontological exposition of the National Museum of Natural History, Paris

Fig. A.33. The shed antler of *Praemegaceros obscurus* from Salcia (Moldova): A, lateral view; B, medial view; C, upper view

Fig. A.34. *Praemegaceros* and related genera: A, *Panolia eldii*; B, *Praemegaceros obscurus* from Pietrafitta, Italy (IGF 4024); C, *Praemegaceros obscurus* from Rotbav Silverstu, Romania; D, *Praemegaceros dawkinsi* from the Forest Bed Formation, England; E, *Candiacervus devosi* (adapted from van der Geer, 2018); F, *Praemegaceros pliotarandoides* from Aliakmon, Greece (adapted from Melentis, 1967). Abbreviations: bs, basal tine; ds., dorsal tine; m., middle tine; p., posterior tine; cr. crown tines

Fig. A.35. The antler vauplan of *Praemegaceros* (*Nesoleipoceros*) *cazioti* (A) and *Praemegaceros* (*Nesoleipoceros*) *solilhacus* (B); abbreviations: *b*., basal tine; *m*, middle tine; *p*., posterior tine; *cr*., crown tines

Fig. A.36. The left hemimandible of *Praemegaceros* (*Orthogonoceros*) *pliotarandoides* (De Alessandri, 1903) from the late Early Pleistocene of Apollonia-1, Greece

Fig. A.37. The antlered skull of a young adult male IGF 243 (MGUF) of *Cervus nestii* (Azzaroli, 1997) from Figline; oblique view

Fig. A.38. The distal fragment of antler of *Cervus canadensis* from the Paleolithic site of Climăuți (Moldova)

Fig. A.39. Modern and fossil subspecies of *Cervus canadensis*: A, *Cervus canadensis sibiricus*, frontal view (adapted from Stepanova and Argunov, 2016); *Cervus canadensis combtayicus*, frontal view; C, upper view of the distal portion of antler

Fig. A.40. *Megaceroides algericus* (Lydekker, 1890): the male skull from Guyotville (now Ain-Benian, Algeria) stored in Paris (NMNH, "Collection of Arambourg", no number): A, side view; B, frontal view; C, palatal view. Scale bars: 5 cm

List of abbreviations

Institutions:

GSUT, the Geological School of the University of Thessaloniki, Greece.

ISB, the Institute of Speleology “Emil Racoviţă”, Bucharest, Romania.

IZC, the Institute of Zoology, Chișinău, Moldova.

IZW, the Institute of Zoology of the University of Wroclaw, Poland.

LPUB, the Laboratory of Paleontology, University of Bucharest, Romania.

MCP, the Musée Crozatier au Puy-en-Velay, France.

MGUF, the Museum of Geology and Paleontology of the University of Florence, Italy.

MNHK, the National Museum of Natural History, Kiev, Ukraine.

MNHN, the Muséum national d'Histoire naturelle, Paris, France.

MNP, the musée national de Préhistoire, les Eyzies-de-Tayac, France.

MPS, the Museum of Paleontology of the Department of Earth Sciences, the University of Rome “Sapienza”, Italy.

NHMB, the Natural History Museum “Grigore Antipa”, Bucharest, Romania.

NHML, the Natural History Museum of London, the United Kingdom.

NHMUF, the Natural History Museum “La Specola”, University of Florence, Italy.

NMENH, National Museum of Ethnography and Natural History, Chisinau, Moldova.

PIN, the Paleontological Institute, Moscow, Russia.

PMUL, the Paleontological Museum of the University “Claude Bernard” Lyon 1, France.

RMO, the Regional Museum “Oltenia” Craiova, Romania.

RMPM, the Regional Museum of Prehistory of Menton, France.

RSU, the Rostov-upon-Don State University, Russia.

SMNH, the State Museum of Natural History of Stuttgart, Germany.

TMH, Teylers Museum, Haarlem, the Netherlands.

Measurements and anatomical points:

BRG, bregma point; CBL, condylobasal length of skull; CDL, condylodental length of skull; CFR, circumference; D, breadth or thickness; DAP, anderoposterior diameter; DLM, lateromedial diameter; DVD, dorsoventral diameter; H, height; L, length; MM, molar series; NS, nasion point; OP, opisthocranion point; ORB, orbit; PP, premolar series; PR, prosthion point; RN, rhinion point.

The abbreviations used for different types of deer antlers:

1) red deer *Cervus elaphus* and related species: BR., brow tine; BZ., bez tine; TR., trez tine; CR., crown tines; PR, pearling;

2) the genus *Praemegaceros*: SB., subbasal tine; B., basal tine, DS., dorsal tine; M., middle tine; P**.** posterior tine; CR., crown tine; PL**.**, palmation;

3) the most of cervids with complicated antlers the general scheme is used: B., basal tine; M., middle tine; B., posterior tine; CR., crown tine; AP**.**, accessory prong;

4) For small two or three tined antlers (muntjacs and similar deer) a simple indication is applied: the first (AN1, anterior) tine, the second tine (AN2, anterior tine of the distal fork), and the third tine (PS3, posterior tine of the distal fork);

5) subfamily Capreolinae: FT, first tine; DF, distal fork; AT, anterior tine of distal fork; PT, posterior tine of distal fork; PR, pearling; PL, palmation;

Other abbreviations:

MAX, maximum; MIN, minimum; N, number or sample size; M, mean value; SD, standard deviation; PROX, proximal; DIST, distal; SIN, left; DX, right.

INTRODUCTION

The topicality and importance of the subject of the thesis. The family Cervidae is among the most successful and species-rich taxonomic groups of large-sized herbivores in modern faunas of Eurasia and the Americas. Modern deer are the most diverse group of herbivores in the Palearctic. In the geological past, the family Cervidae was represented by a significantly wider variety of evolutionary and ecological forms, including many extinct forms that provide numerous biogeographic and evolutionary examples of parallelism, convergence, extreme specializations, explosive evolutionary radiation in newly colonized areas such as South America, evolution in conditions of insular isolation, and the emergence of endemic forms in continental biogeographic refugia (Lydekker, 1898; Azzaroli, 1961; Gliozzi and Malatesta, 1982; Lister, 1987; Vislobokova, 1990; Geist, 1998; Croitor, 2014, 2018a; Croitor et al., 2006).

The dissertation focuses on the taxonomy, systematics, and evolution of the so-called "crown deer" (sensu Azanza et al., 2013; Amson et al., 2015; Mennecart et al., 2017). Crown deer are representatives of the subfamilies Cervinae and Capreolinae, as well as their direct forerunners, from the Late Miocene to Pleistocene of Europe, the Near East, and North Africa. Crown cervids are differentiated from the "archaic" stem cervids by several evolutionary traits that are found in modern deer: 1) the cranial appendages are relocated from the orbital area to the more posterior frontal position, with their basal portion being an outgrowth of frontal bones; 2) the distal portion of cranial appendages is a regularly shed part that regenerates from the apices of pedicles; and 3) the basal part of the shed portion of cranial appendages is characterized by the development of a burr, which is a bony rim at the base of the antlers that seals the pedicle skin and appears with the first subsequent antler (Bubenik, 1990).

The description of the research domain state and the identification of research problems. Simpson (1945) noted that the classification of the family Cervidae raises many unresolved questions. The known diversity of fossil cervid forms significantly increased since Simpson's (1945) monographic work on the mammalian classification was published. During the last decades, important contributions to the understanding of the evolution and phylogeny of fossil deer from the western Palearctic have been made by Azzaroli (1947, 1952, 1953, 1961, 1979, 1985, 1992, 1994), Kahlke (1956, 1963, 1965, 1969, 1997, 1999, 2001), Czyżewska (1960, 1968), Kototkevich (1963, 1964 a, b, 1970, 1974, 1988), Heintz (1970), Vislobokova (1986, 1990, 2009, 2012, 2013), Lister (1987, 1990, 1993, 1994, 1999), Azanza (1995; 2000); Stefaniak (1995, 2001, 2007, 2015), and van der Made (1998, 1999, 2003, 2006, 2014) and other students who collected a large amount of data on cervid paleontological record from the western Palearctic.

Despite the great abundance and diversity of fossil cervid species, their evolutionary and systematic interpretations are rather contradictory, and relationships with the living species remain unclear and speculative. In most cases, the difficulties in cervid classification arise from 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 complicated by numerous synonymies, taxonomic confusions, and poor definitions of genera.

Another important challenge is the absence of methodologically uniform criteria applied in the taxonomy and systematics of modern and fossil cervids. The taxonomy and systematics of modern deer are based on the combination of antler and cranial morphology (Flerov, 1952). Traditionally, the taxonomy of fossil deer is mostly based on antler morphology (Azzaroli, 1952; Heintz, 1970), which is a major methodological constraint. Although cervid antlers reflect the ethological diversity of cervid species and thus ensure genetic isolation between them, they are characterized by ontogenetic, geographic, and individual variability that led to a large number of synonymous species names based on variable and often fragmentary antlers (Heintz, 1970; Croitor, 2018b).

The shape of antlers is influenced by multiple factors of different nature (ecophysiological, morphofunctional, biomechanical, environmental, social, etc.) that are still insufficiently understood (Bubenik, 1990). Therefore, many fossil species remain poorly defined, and many fossil deer remains, even if represented by fine cranial material that contains valuable taxonomic information, remain poorly understood. Although cranial morphology is an important source of taxonomic information in neontology, fossil craniological material is often disregarded because of the rather uniform cervid cranial morphology and relatively rare well-preserved fossil cranial findings associated with antlers. This incomplete and disregarded record of the cranial morphology of fossil deer is another constraint for cervid taxonomy at the genus level (Vislobokova, 1990).

Recent advances in the molecular phylogeny of cervids have provided exciting evidence on the phylogenetic relationships among modern deer and revealed the systematic position of some peculiar cervids, such as the antlerless *Hydropotes inermis*, or *Elaphurus davidianus*, which is characterized by very unusual antlers (Miyamoto et al., 1990; Douzery, Randi, 1997; Randi et al., 1998; Pitra et al., 2004; Gilbert et al., 2006). However, the phylogenetic and systematic positions of many fossil cervids, such as the group of "giant deer," the Plio-Pleistocene "*Dama*-like" deer with simple three-pointed antlers, and the Late Miocene "pliocervines," remain speculative.

The purpose of this study is to determine the systematic position of fossil cervids from the Late Miocene to the Pleistocene in the western part of the Palearctic zoogeographical realm (including Europe, the Near East, and North Africa), as well as to investigate their evolution, paleobiogeography, and phylogenetic relationships with modern deer. The research is based on fossil deer material from "historical" paleontological collections in Europe, which contain a large number of fossils from across the European continent and North Africa, collected over the last two centuries. The Western Palearctic biogeographic zone was chosen as the basis and framework of the research due to the geographical distribution of the collected data. However, the paleobiogeographic approach is of particular interest as it allows for the investigation of evolutionary changes in various cervid lineages in the context of geological and climatic evolution. The Late Miocene and Pliocene of western Eurasia are particularly important geological periods during which the main features of the modern Palearctic zoogeographic realm emerged (Croitor and Brugal, 2007).

The objectives of the present study are focused upon the revision of the original type material and the verification of all taxonomic acts that represent the basis of the currently accepted views on the systematics of the family Cervidae.

1) The revision of the original material that served for descriptions of species. The most important historical collections studied are the 'Collezioni Granducali' (MGUF), which includes most of the type material from the Upper Valdarno (Tuscany, Italy), the historical collection from the Cromer Forest-bed Formation in England (NHML), and the historical collection from Perrier-Etouaires in France (MNHN). Heintz (1970) conducted a detailed taxonomic revision of cervid species from the Pliocene of Perrier-Etouaires, and Azzaroli (1947, 1992) and Azzaroli and Mazza (1992a) published a series of articles on the revision and redescription of deer species from the Upper Valdarno. Azzaroli (1953, 1994) revised the historical collection of fossil deer from the Cromer Forest-bed Formation, and Lister (1993) proposed stratigraphic interpretations of cervid remains from this formation. Dong (1996) carried out the taxonomic revision of Ruscinian (Early Pliocene) deer from Languedoc and Roussillon (France). Unlike previous works, the present study proposes the inclusion of cranial material in the taxonomic study, following the methodology and criteria of modern zoological studies (Pocock, 1943 a, b, c; Flerov, 1952; Sokolov, 1959; Bouvrain et al., 1989).

2) The revision of original descriptions of taxa and the verification of taxonomic acts. This is an important stage of research focused upon the analysis of the original bibliographic sources with taxon descriptions and the analysis of all subsequent scientific publications that modify the taxonomic status of name-bearing specimens (types) or a taxon rank. The ultimate objective is to carry out the analysis of the taxonomic history of name-bearing specimens and related taxa in order to eliminate taxonomic confusions. This stage aims to track the taxonomic status of a name-bearing specimen through a sequence of taxonomic acts proposed by various authors and to estimate the significance of those acts, their priorities, and their validity according to the rules of the International Code of Zoological Nomenclature (ICZN, 2012).

3) The taxonomic revision of species and higher rank taxa (genera, tribes, subfamilies). The taxonomic revision of a genus includes the redescription of its genotype (a species that srved for a genus description), the updated list of species included in the genus, and the geographical and geological distributions. The taxonomical revision of tribes and subfamilies concerns mostly the evaluation of their taxonomical rank, diagnostic characters, and the genera included in the taxon.

4) Emended diagnoses of species or taxonomic groups of higher level. Due to the specific nature of paleontological material, the taxonomy of fossil cervids is somewhat akin to the "splitting" approach used in the systematics of modern deer, with antler characteristics being the predominant diagnostic feature in systematic paleontology (Croitor and Robinson, 2020). In this study, the revised diagnoses of extinct cervid species and genera are complemented by cranial diagnostic features. The updated and complete diagnoses ensure the accuracy of the definition of an extinct cervid taxon, which should closely correspond to the criteria used for modern deer species and genera. This approach helps bridge the taxonomic gap between modern and extinct deer taxa.

5) The systematic position and phylogenetic relationships of fossil crown deer from the western Palearctic. Modern molecular genetic studies significantly advanced our knowledge of phylogenetic relationships among modern deer (Douzery and Randi, 1997; Polzein and Strobeck, 1998; Randi et al., 1998; Kuznetsova et al., 2005; Gilbert et al., 2006) but raised the question on the adequacy of the morphology-based systematical models (Groves, 2013). Nonetheless, the analysis of the bony labyrinth morphology of modern and fossil deer provided reliable results on the phylogenetic relationships between some fossil and modern cervids (Mennecart et al., 2017). The present study proposes to use morphological characters that have been formally diagnosed as taxonomically significant (antler, cranial, dental, and some postcranial morphological characters) with the purpose to reveal phylogenetic affinities among fossil and modern cervid taxa. The study is based on the multivariate cluster analysis of the diagnostic cranial, dental, antler, and some selected postcranial characters and allows for the evaluation of the taxonomic importance of diagnostic characters and reveals the systematic position of fossil species and questionable groups of higher taxonomic rank (Pliocervinae and Megacerini).

6) The evolutionary, paleobiologic, and paleoecologic analysis of the crown cervids from the western Palearctic. The taxonomic and systematic value of a morphological feature can be difficult to understand, especially in highly specialized endemic species with modified initial bauplan of antlers, dentition, and skull shape. The morpho-functional and eco-morphological approach is useful for understanding specialized features, such as simplified antlers or unusual skull proportions. Through ecomorphological and morpho-functional analyses of an extinct species' adaptations, we can distinguish plesiomorphic taxonomically important characters from apomorphic features that reflect the evolutionary response of a deer species to environmental conditions and/or geographic isolation. These factors can include the founder effect, genetic drift, evolutionary interactions and co-adaptation with other species (predators, competitors), and their combinations. Individual variation can also be helpful for understanding evolutionary antler specializations, especially if individual morphological variants show vestiges of reduced parts of antlers or reveal the initial antler bauplan (Croitor, 2006a).

7) Paleobiogeography of the family Cervidae in the western Palearctic. Geological transformations, geographic conditions, and climate shifts have greatly influenced the evolution, diversification, and dispersals of the family Cervidae. The closure of the Panama Isthmus caused important global climate changes during the period 4.6-2.8 million years ago, which affected the climate evolution of the western Palearctic. The transport of heat and moisture by the Gulf Stream from tropical latitudes to the Northern Atlantic caused the Early Pliocene warming of the Northern Hemisphere, an increase in climate humidity in western Eurasia, and the intensification of the Northern Hemisphere glaciation (Haug and Tiedemann, 1998; Denk et al., 2013; O'Dea et al., 2016). These global changes greatly influenced the evolution and paleobiogeography of the family Cervidae in the Western Palearctic. Special attention is given to the importance of the Gulf Stream's influence on the paleobiogeography of fossil cervids during the Plio-Pleistocene epoch.

The research hypothesis. Both subfamilies Cervinae and Capreolinae passed through the holometacarpal stage of limbs (the lateral metacarpals II and V are complete), following different types of reduction of lateral metacarpals. The evolutionary radiation of Capreolinae took place in western Eurasia during the Late Miocene. Holometacarpal representatives of the subfamily Capreolinae are characterized by the stronger reduction of proximal portions of their lateral metacarpals, the dichotomous type of antler bauplan (all ramifications of antlers represent dichotomous bifurcations), the post-glenoid foramen that is not surrounded by the squamosal bone (its posteromedial edge is constituted by a lateral expansion of the petrous bone), and a set of dental specializations. The evolution of dentition in Capreolinae is characterized by the following features: 1) the morphological reinforcement of the premolar series that remains relatively long and tends partially to acquire the grinding function: the lower fourth premolar (P_4) becomes molarized at a very early evolutionary stage; the third lower premolar (P_3) also may attain the advanced degree of molarization in some genera; 2) the lower molars in early representatives of

Capreolinae are supplemented with the *Palaeomeryx* fold; 3) the upper molars in most of Capreolinae are supplemented with an additional protoconal fold. The Late Miocene evolutionary radiation of Capreolinae was represented by the cervid forms with primitive two-pointed antlers (*Lucentia*) and more advanced forms with three (*Procapreolus*) and more antler tines (*Pliocervus*, *Damacerus*, *Metadicrocerus*, *Neomegaloceros*). By the end of the Miocene, most of the Capreolinae forms from western Eurasia became extinct. *Procapreolus* and *Croizetoceros* are the representatives of the Late Miocene radiation of Capreolinae that survived until the Upper Pliocene and Early Pleistocene, respectively. The geographic centers of the evolution of modern representatives of the Old World Capreolinae (*Rangifer*, *Alces*, *Capreolus*, and *Hydropotes*) were located in the middle latitudes of the eastern part of Eurasia.

The evolutionary radiation of plesiometacarpal deer (the subfamily Cervinae) took place in Southeast Asia during the Late Miocene and, unlike Capreolinae, maintained its original diversity until pesent days. The closure of the Isthmus of Panama caused the important transport of tropical warmth and humidity into the North Atlantic and triggered the Pliocene climate humidification in western Eurasia. This global climate transformation favoured the dispersals of the representatives of the subfamily Cervinae (*Praemuntiacus*, *Metacervocerus*, *Praeelaphus*, *Rucervus*) from the area of their initial evolutionary radiation (Southeast and East Asia) to western Eurasia. Cervinae are characterized by a set of antler, cranial, dental, and postcranial characters that distinguish them from Capreolinae and indicate a different ecological strategy and evolutionary specialization. The holometacarpal condition is still retained in the earliest representatives of the subfamily Cervinae but shows an evolutionary trend toward the plesiometacarpal condition, as their lateral metacarpals progressively lost distal portions, including articulations with lateral phalanxes. The antler bauplan is characterized by the main axis (the beam) that is supplemented by a rather low-positioned basal ramification and, in the more advanced stages of antler evolution, further distal ramifications that always have a secondary character to the main antler axis. The post-glenoid foramen is surrounded by the squamosal bone. The dentition of Cervinae is characterized by the general trend toward the shortening of the premolar series that tends to maintain the initial shearing function. The lower fourth premolar is often primitive and unmolarized, and only in some genera, it attains a certain degree of molarization, that never reaches the high degree of specialization characteristic of Capreolinae. Unlike Capreolinae, the lower third premolar is never molarized. The *Palaeomeryx* fold in lower molars is never developed. The additional protoconal fold is developed only in some Pleistocene forms. The plesiometacarpal deer dispersed for the first time into western Eurasia during the Early Pliocene after mass extinction of telemetacarpal deer, which were represented in the Plio-Pleistocene record by few survived lineages. The dispersal of Pliocene plesiometacarpal deer into western Eurasia was chronologically very close to the first dispersal of Cervinae into the Indian Subcontinent. One can assume that the evolutionary and ecological diversification within the Cervinae branch also was an important factor that favoured the Pliocene dispersals of plesiometacarpal deer.

The research methodology applied in the present study is based on the taxonomic verification and revision of extinct cervid species, the record of cranial, dental, and antler characters, and the cluster analysis of morphological characters.

Special attention is focused on the well-preserved fossil cranial material, which provides the most important diagnostic characters and systematical information at the genus level (Vislobokova, 1990). Both the morphological characteristics (the description of a condition of selected anatomical parts) and the biometrical data are collected. The considered morphological craniodental characters are broadly used in neontological taxonomy and systematics (Flerov, 1952; Sokolov, 1959). The taxonomical values of diagnostic characters are adjusted in accordance with molecular phylogeny data. A hierarchical cluster analysis of diagnostic craniodental characters was carried out to estimate the taxonomic and systematic value of the morphological characters used in modern cervid systematics. 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). The applied approach allows to reveal the systematical position of fossil deer among modern representatives of the family Cervidae.

The previous attempts to carry out hierarchical cluster analyses of craniometric data gave inadequate results (Markov and Danilkin, 1999; Meijaard and Grooves, 2004) conflicting with the genetic data (Pitra et al., 2004; Gilbert et al., 2006), therefore this methodological approach was not considered in the present study. The cranial measurements are used in the present study to describe the cranial proportions and the size ratios between various parts of a cranium. The cranial measurements are taken using the anatomical landmarks that permit avoidance of biases caused by the extreme specializations of cranial shape.

Pfeiffer-Deml (2016) challenged the reliability of the cranial morphology for cervid systematics since, according to the cited author, cranial proportions generally are variable and show a certain ontogenetic variation that makes the cranial material unsuitable for the phylogenetic studies. However, the study based on the large sample of modern red deer demonstrated that braincase proportions based on measurements between anatomical landmarks generally do not change during animal’s life (Mystkowska, 1966). Pfeiffer-Deml (2016), nonetheless, pays great attention to some cranial features, such as the length of nasal bones that, according to the cited author, is a "strong argument" for evolutionary relationships between phylogenetically distant cervids. According to Vislobokova (1990), this feature is apomorphic and has a systematic value at the species level. Pfeiffer-Deml (2016) includes all small-sized cervines from the Pliocene and Early Pleistocene of Europe in the genus *Dama*. This conclusion is based mostly on the details of limb bone morphology which are regarded as "plesiomorphic". However, Pfeiffer-Deml (2016) does not explain why certain morphological postcranial characters are regarded as plesiomorphic. The proposed distinction of minor and quite variable morphological details of postcranial bones into plesiomorphic and apomorphic characters remain speculative. Since the postcranial morphology in hoofed animals greatly depends on body mass, locomotion type, and ground surface character (Gambarian, 1972; Köhler, 1993; Curran, 2015), one can assume that the definition of the genus *Dama* proposed by Pfeiffer-Deml (2016) corresponds rather to a group of cervids that evolved in the same adaptive zone (wooded environments with a warm climate of middle latitudes) and developed the similar adaptations, such as the medium-to-small body size (the eco-physiologically optimal body mass for the adaptive zone), the similar locomotion strategy corresponding to the body mass and the landscape conditions (Gambarian, 1972; Scott, 1985), and the similar postcranial morphology that resulted from the evolutionary, environmental, snd biomechanical constraints (Curran, 2015; Alcalde and van der Hoek Ostende, 2014). The large number of modern studies focused on the statistical analysis of ruminant postcranial morphology revealed its strong correlation with paleoenvironmental conditions and body mass (DeGusta and Vrba, 2005a, b; Curran, 2015; Alcalde and van der Hoek Ostende, 2014).

Di Stefano and Petronio (1998) based their systematic study of the small-sized Plio-Pleistocene deer of Europe on the cluster analysis of long limb bone measurements. The obtained results are different from those of Pfeiffer-Deml (2016) and suggest a close relationship between the European extinct cervids to modern *Axis* and *Rusa* (Di Stefano and Petronio, 1998). Therefore, the postcranial material cannot be regarded as a reliable source of systematic and phylogenetic information but indicates species' adaptations to a certain type of environment. Nonetheless, some essential features of postcranial morphology, such as the type of reduction of the lateral metacarpals, represent an important general evolutionary specialization of cervid limbs and are broadly accepted as diagnostic characters of the subfamily level (Simpson, 1945; Vislobokova, 1990).

The novelty and scientific originality of the obtained results: 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 proposes a systematic and taxonomic revision of fossil deer from the Western Palearctic and presents a new phylogenetic model of the crown cervids (subfamilies Cervinae and Capreolinae). For a long time, the origin of telemetacarpal deer (subfamily Capreolinae) remained obscure. Some authors hypothetically related the origin of the subfamily Capreolinae to North American Dremotheriinae in an attempt to explain the missing paleontological record of the early evolutionary radiation of telemetacarpal deer in Eurasia (Vislobokova, 1990; Vislobokova and Kalmykov, 1994). This study reveals the early stages of evolution of the subfamily Capreolinae from the Late Miocene of Europe and clarifies the systematic position of the poorly understood Late Miocene holometacarpal deer from southeastern Europe. The study also clarifies the systematic position of most of the fossil crown deer, including insular and North African endemics.

Fundamentally new results for science and practice obtained. The taxonomic examination of fossil deer from the Late Miocene to the Late Pleistocene in the western Palearctic region has revealed the existence of 27 genera and 78 species. The thesis proposes a new systematic and phylogenetic model for the crown cervids of Eurasia (subfamilies Cervinae and Capreolinae). The proposed phylogenetic relationships among fossil deer from the Western Palearctic are based on the multivariate analysis of diagnostic craniodental (including antlers) characters, a methodological approach that was for the first time applied in the study of fossil cervid systematic relationships. The study of cervid systematic morphology revealed the phylogenetic relationships between the mainland deer forms and their endemic insular Mediterranean relatives. The obtained results permitted to establish two new cervid genera: *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. The revision or fossil material allowed to establish the following new species and subspecies:

Praeelaphus australorientalis Croitor, 2017 (the Pliocene of Ukraine, Moldova and Romania);
Rucervus gigans Croitor, 2018 (the Early Pleistocene of Greece);
Rucervus radulescui Croitor, 2018 (the Early Pleistocene of Romania);
Cervus canadensis combrayicus Croitor, 2020 (the Late Pleistocene of France).

Theoretical significance: the study reveals the emergence and development of the Palearctic biogeographic realm in the western part of Eurasia and North Africa. The obtained results on the evolution of deer antlers, their ecomorphology, and functional morphology reveal the relationship between deer antler morphology and social behavior and environmental conditions. This information sheds light on how deer have adapted to their environments over time. The systematic and morphological study revealed the systematic position of the holometacarpal deer and permitted us to reconsider the validity of some taxonomic groups at the family level. The study highlights the importance of southern glacial refugia in the evolution and diversification of cervid fossil forms, as well as describes the most common mechanism of extinctions of fossil deer related to the general ecological and evolutionary strategy of the family Cervidae.

The applicative importance of the thesis: the results obtained from this study allow us to understand the mechanisms by which climate change has influenced the taxonomic diversity and extinctions of cervid species in the past. By revealing the origin and systematic positions of fossil cervids, we can correlate their dispersals and evolution with major geological events and use them as biostratigraphic markers. The results obtained on the systematics and phylogeny of fossil cervids also enable us to understand the origin of the taxonomic diversity of modern species, as well as the status of some threatened modern deer.

The main scientific results presented:

1. The holometacarpal deer from the Late Miocene of western Eurasia represents the early evolutionary stage of telemetacarpal deer (subfamily Capreolinae).
2. The subfamily Pliocervinae is an artificial and 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 plesiometacarpal deer from the Pliocene of western Eurasia represents the early evolutionary radiation of the subfamily Cervinae from southeastern 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 parallelism of morpho-functional adaptations that minimize health damage, wounding, and death during the rutting season.
7. The general ecological and evolutionary strategy of the family Cervidae is one of the most common causes of the Palearctic deer species' extinction in the past through the mechanism of ecological exclusion.

Implementation of scientific results: The results obtained from the study of systematics, evolution, and dispersals of fossil deer from the western Palearctic have been used to facilitate biostratigraphic regional correlations in the Republic of Moldova and Romania (Croitor et al., 2020; Terhune et al., 2020), to understand paleobiogeographic changes in Europe influenced by climate changes (Croitor, 2017), and to aid in paleoecological reconstructions (Kaizer and Croitor, 2004; Curran et al., 2021). These results have also helped to provide a paleoecological and paleobiogeographic context for the dispersal and subsistence of early hominins in Europe (Croitor, 2017; Croitor et al, 2019). The findings from archaeozoological expertise have been included in the archaeological reports of the State University of Moldova, the National Archaeological Agency, the Institute of Cultural Heritage, and the University of Barcelona.

Approval of scientific results. The main results and conclusions obtained on the topic of the thesis were communicated and discussed at the following scientific meetings: Sixth International Congress of Vertebrate Morphology – Jena, Germany, 2001; Verhandlungen der Gesellschaft fur Okologie, Band 32: 465; Cottbus, Germany, 2002; "Regional developments and interregional correlations" - 18th International Senckenberg Conference – VI International Palaeontological Colloquium in Weimar, Germany, 2004; "Cadre biostratigraphique de la fin du Pliocène et du Pléistocène inférieur (3 Ma à 780 000 ans) en Europe méridionale", International Colloque, Tende, France, 2005; "Problems of palaeontology and archaeology of the south of Russia and neighbouring territories". International conference INQUA, Rostov-upon-Don – Azov, Russia, 2005; "Le Quaternaire, Limites et Specificites", Colloque international Q5, Paris, 2006; Romanian Symposium on Paleontology, the VI-th edition, Iaşi, Romania, 2007; XVII INQUA Congress – Cairns, Australia, 2007; Seventh Romanian Symposium on Palaeontology, Cluj-Napoca, Romania, 2009; "European Middle Palaeolithic during MIS 8 – MIS 3, culture – environment – chronology", International Conference Wolbrom, Poland, 2012; XIV-th Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP), Haarlem, The Netherlands, 2016; "Taphonomie Quaternaire: du General au Particulier", 4th ICAZ Taphonomy Working Group Meeting, Paris, 2016; "Sustainable use, protection of animal world and forest management in the context of climate change", IX-th International Conference of Zoologists, Chișinău, Moldova, 2016; The Fossil Week", 5-th International Paleontological Congress – Paris, 2018; "Palaeontology in the virtual era", the 2-nd Palaeontological Virtual Congress, 2020.

Publications on the topic of the thesis: the results of the thesis are presented in 70 publications, including 1 monography, 2 chapters in a collective monography, 29 articles in international scientific articles with impact factor, 15 articles in recognised foreign scientific journals, 10 articles in journals from the National Register of specialized journals, 4 articles in scientific collections, 22 abstracts at scientific meetings abroad and 4 abstracts of presentations made at national scientific meetings.

The volume and structure of the thesis: the thesis consists of 208 pages and includes the introduction, 6 chapters, conclusions, scientific recommendations, a bibliography with 348 references, and annotations in English, Romanian, and Russian.

Summary of the chapters of the thesis. The introduction chapter, “The historical overview and the current views on the cervid systematics and phylogeny,” aims to demonstrate the evolution of views and methodological approaches to the systematics and phylogeny of the family Cervidae. This historical overview helps to understand the diversity of opinions on fossil deer systematics in the context of the general advancement of the natural history sciences, the increase of paleontological data, and the advancement of available research tools. The historical analysis of the views on fossil deer systematics and evolution allows us to understand the objective constraints and methodological difficulties, and to gain an understanding of the current problems in cervid systematics and phylogenetic relationships in order to find methodologically reliable solutions.

The applied methodological solutions are described in the chapter “Methodological approach to the study of cervid systematics and phylogeny". This chapter also provides information on the geochronological frames of the paleontological material included in the study. The chapter “Systematic diversity of crown cervids (family Cervidae Goldfuss, 1820) in Western Palearctic” presents the taxonomic analysis of Cervidae findings from the Late Miocene to the Late Pleistocene of the Western Palearctic, which includes the context of the original description of a taxon, the historical description of taxonomic acts, the synonymy, and the detailed morphological description of cervid species.

The chapter “Main evolutionary features of crown cervids from Western Palearctic” presents the synthesis of cervid evolution from Europe, the Near East, and North Africa based on the general evolutionary and biological strategy of the family Cervidae and the context of changing climate and associated faunas. The chapter “Matching fossil record and molecular phylogeny data” aims to juxtapose the proposed systematic and phylogenetic models of cervids from the Western Palearctic in the present study with molecular phylogeny data based on modern cervid species. This juxtaposition permits estimating the reliability of the methodological approach used in the present study.

The chapter “Paleobiogeography of deer from the Western Palearctic” discusses the historical development and diversity of the family Cervidae in the zoogeographic area under consideration in the context of changing climate and geographical conditions.

1. THE HISTORICAL OVERVIEW AND THE CURRENT VIEWS ON THE CERVID SYSTEMATICS AND PHYLOGENY

1.1. Historical overview of studies on cervid systematics

The earliest publications from the 17th and 18th centuries that described fossil deer were brief notes and reports on natural curiosities, such as Knowlton (1746) and Barker (1785). While these early descriptions of cervid fossils were not accurate enough, they did provide a scientific basis for subsequent systematic studies of fossil deer. Following the systematic classification paradigm of that epoch, all cervid species described by the 18th century were included in the genus *Cervus* (Linnaeus, 1766). However, from then until the middle of the 20th century, the genus *Cervus* was often viewed as an arbitrary taxonomic solution for insufficiently known or poorly understood forms of cervids.

Gray (1821) established the family Cervidae as a systematic group of ruminants characterized by the development of solid frontal deciduous processes covered with deciduous skin. Gray (1821) included the genera *Alces* and *Capreolus* in addition to *Cervus* in Cervidae.

Cuvier (1823) conducted the first important study of fossil deer, publishing an overview of all known fossil cervid forms, mostly from the Quaternary. Despite many important paleontological discoveries made since the 19th century, our knowledge of fossil deer evolution has advanced to a lesser degree. Vague, incomplete, or imperfect original descriptions of species cause taxonomical confusions complicated by multiple synonymies and lack of methodologically uniform criteria in the taxonomy and systematics of fossil deer. Many fossil cervid forms remain little known, poorly understood, or misinterpreted. Despite the great variety of proposed cervid classification schemes and phylogenetic models, visible progress is impeded by incomplete and confused taxonomical data.

Brooke (1878) made the first attempt to build a solid classification of the family Cervidae by describing two types of reduction of the second and fifth metacarpals in modern cervids, represented by their proximal (plesiometacarpal condition) or distal (telemetacarpal condition) remnants. The type of reduction of lateral metacarpals reflects two different directions of adaptation to cursoriality and is one of the most essential characteristics that splits modern cervids into two subfamilies: Cervinae and Capreolinae. Representatives of the subfamily Cervinae have completely lost the distal parts of their lateral (second and fifth) metacarpals but retain proximal vestiges of those bones (the plesiometacarpal condition). Deer of the subfamily Capreolinae are characterized by a different type of lateral metacarpals reduction, retaining only their distal portions (the telemetacarpal condition) (Brooke, 1878). The work of Brooke (1878) was thoroughly discussed and even criticized in subsequent publications by Lydekker (1898), but it remains one of the most important systematic studies of the family Cervidae confirmed by modern systematic approaches.

According to the reduction type of lateral metacarpals, Brooke (1878) established two informal groups of cervids: the "Plesiometacarpi" group, which includes all Old World deer except for *Capreolus* and *Hydropotes*, and the "Telemetacarpi" group, which includes mostly New World deer (except for *Cervus canadensis*), as well as the Old World genera *Capreolus* and *Hydropotes*, and the circumpolar and circumboreal genera *Rangifer* and *Alces*. Brooke (1878) also noted a correlation (with a few exceptions) between the telemetacarpal morphological condition and the complete dividing of nasal cavities by a vertical plate of vomer, in combination with some other morphological characters, giving zoogeographic, systematic, and phylogenetic importance to the observed characters. In most of the telemetacarpal deer, according to Brooke (1878), the vomer is prolonged downwards and backwards to become ankylosed to the palatal bones and thus dividing the nasal cavity into two distinct chambers. Brooke (1878) notes that the nasal cavity is not divided by vomer in three Old World telemetacarpal deer (*Capreolus*, *Alces*, and *Hydropotes*), which consequently were regarded in Brooke's classification as a group of deer with the uncertain position. Brooke (1878) also suggested that the bone septum completely dividing the nasal choanae in American deer is a primitive character shared with less specialized artiodactyls such as *Hippopotamus*, *Sus*, and *Tragulus*. Brooke's (1878) terms "Plesiometacarpi" and "Telemetacarpi" are not available according to the rules of ICZN, but they were later considered as equivalents of cervid subfamilies Cervinae Goldfus 1820 and Capreolinae Brookes, 1828 (= Odocoileinae Pocock, 1923), respectively (Frick, 1937; Grubb, 2000; Gilbert et al., 2006).

. Lydekker (1898) ignored the taxonomic significance of the type of lateral metacarpal reduction in cervids and proposed a simplified classification of the family Cervidae, which contained only two subfamilies: the subfamily Cervinae ("the true deer") with all modern genera of plesiometacarpal and telemetacarpal deer, as well as the extinct genera *Dremotherium*, *Dicrocerus*, and *Anoglochis*, and the subfamily Moschinae ("the aberrant deer") with the single genus *Moschus*. Lydekker (1898), however, admits that the subfamilies Cervinae and Moschinae can be regarded as families, while cervid genera may be grouped into subfamilies. Lydekker (1898) believed that antlers should hold a higher value in cervid classification. He recognized two main types of antlers in Cervidae: the "brow-tined" type and the "forked" type that generally correspond to Dawkins' (1878) "Axeidae" and "Capreoli". However, Lydekker (1898) did not propose a formal taxonomical distinction based on the dichotomy in cervid antler structure. He noted that the Old World telemetacarpal deer (*Rangifer*, *Alces*, *Capreolus*) are morphologically and taxonomically quite isolated.

Pocock (1910) attributed the status of subfamily to the plesiometacarpal (Cervinae) and telemetacarpal deer (Capreolinae), but later (Pocock, 1923) divided the telemetacarpal deer into several subfamilies (Alcinae, Capreolinae, Hydropotinae, Odocoileinae, Pudinae, Rangiferinae), returning to the informal division of Cervidae into Telemetacarpalia and Plesiometacarpalia.

Simpson (1945) proposed the first important systematical generalization of cervids that greatly influenced the modern paradigm of the systematics of the family Cervidae. Simpson (1945) included all modern telemetacarpal deer and some fossil forms in the subfamily Odocoileinae Pocock, 1923. He recognized six main branches, or subfamilies, in the composition of the family Cervidae: Palaeomerycinae Mathew, 1904; Moschinae Zittel, 1893; Dromomerycinae Frick, 1937; Muntiacinae Pocock, 1923 (including Simpson's new tribe Dicrocerini with the type genus *Dicrocerus*; the genera names *Heteroprox* Stehlin, 1928, and *Euprox* Stehlin, 1928 were included in the synonymy of *Dicrocerus*); Cervinae Baird 1857 (including Pliocervinae Khomenko, 1913); and Odocoileinae Pocock, 1923 (including Capreolidae Brookes, 1828; Alcinae Jerdon, 1874; Rangiferinae Pocock, 1923; and Hydropotinae Trouessard, 1878). According to Simpson (1945: p. 267), the phyletic relationship between *Dicrocerus* and *Muntiacus* is not certain, however, those genera represent a similar evolutionary stage and it is at worst a convenient morphological grouping of these and other similar cervids in the subfamily Muntiacinae. Vislobokova (1990) and Webb (2000) generally accepted Simpson's (1945) systematic division of Cervidae but made a modification by excluding elks and Chinese water deer from the subfamily Odocoileinae and placing them in the subfamilies Alcinae Jerdon, 1874 and Hydropotinae Trouessart, 1898, respectively.

Flerov (1952) divided the cervid family into five subfamilies, disregarding the plesiometacarpal and telemetacarpal division: Palaeomerycinae Matthew, 1904 (including *Dremotherium* and *Palaeomeryx*); Dromomerycinae Frick, 1937; Cervulinae Sclater, 1870 (= Muntiacinae); Cervinae Baird, 1857 (including *Pliocervus*, *Cervavitus*, *Procapreolus*, *Capreolus*, and *Alces*); Neocervinae Carette, 1922 (= Capreolinae Brookes, 1828, = Odocoileinae Pocock, 1923); and *Hydropotinae* Trouessard, 1898. According to Flerov (1952), the Late Miocene *Cervavitus* represents a transitional link between the muntjac-like *Dicrocerus* and the modern *Cervus* and other closely related Cervinae forms, while the arbitrary group of the "American deer" resulted from the local evolutionary process of Miocene *Blastomeryx*. Flerov (1952) proposed also the hypothesized phylogenetic relationships of modern cervids with the fossil forms.

Azzaroli (1953) proposed a similar classification for the living deer, which are divided into seven subfamilies: Cervinae Baird, 1857; Muntiacinae Pocock, 1923; Capreolinae Brookes, 1828; Odocoileinae Pocock, 1923; Rangiferinae Pocock, 1923; Alcinae Jerdon, 1874; and Hydropotinae Trouessard, 1898.

According to the traditional views, the paleontological record does not give clear answers on the origin of telemetacarpal deer and phylogenetic relationships between the modern Capreolinae genera. The earliest representatives of *Alces*, *Capreolus*, and *Rangifer* appear in the Pliocene and Early Pleistocene of Asia and already show the specialized features characteristic of those genera (Vislobokova et al., 1995; Webb, 2000; Bondarev et al., 2017).

Nonetheless, the systematic models based on living cervid forms could not give answers on systematical positions of very diversified and peculiar fossil forms, as many of them do not have evolutionary and eco-morphological analogues in modern faunas. Those fossil cervid forms were placed in separate taxonomic groups. Two important family group taxa were created for the fossil deer forms that have no analogues in the modern animal world: the subfamily Pliocervinae Khomenko, 1913, which was regarded as a group of transitional forms between the primitive muntjac-like deer and advanced "true "deer, and the tribe Megacerini Viret, 1961 that grouped the giant forms of deer of the subfamily Cervinae and their supposed smaller relatives. Those taxonomic groups were accepted uncritically, although their relationships with other cervid taxonomic groups remained rather speculative (Croitor, 2016, 2020).

Groves and Grubb (1987) proposed the division of modern deer into three subfamilies (Hydropotinae, Odocoileinae, and Cervinae). Later, Groves and Grubb (1990) included muntjacs in a separate family, Muntiacidae. According to the updated classification by Grubb (2000), the family Cervidae includes the following subfamilies: Hydropotinae Trouessart, 1898; Lagomerycinae Pilgrim, 1941 (with tribes Lagomericini Pilgrim, 1941 and Dicrocerini Simpson, 1945); Pliocervinae Symeonidis, 1974 (with genera *Cervavitus* and *Pliocervus*); Capreolinae Brookes, 1828 (with tribes Capreolini Brookes, 1828; Odocoileini Pocock, 1923; Alceini Brookes, 1828; Rangiferini Brookes, 1828); and Cervinae Goldfus, 1820 (with tribes Muntiacini Knotterus-Meyer, 1907 and Cervini Goldfuss, 1820). Grubb (2000) included in the tribe Muntiacini only modern muntjacs from Southeastern Asia and the extinct Chinese genus *Eostyloceros*. Grubb (2000) was the first who confirmed the polyphyletic nature of the informal group of “primitive” muntjac-like cervids and treated them as members of two different subfamilies: Lagomerycinae and Cervinae.

The systematic work of Bouvrain et al. (1989) is remarkable for the complex methodological approach that involved the karyotype, morphological, and biochemical data. The results obtained by Bouvrain et al. (1989) supported the monophyly of the subfamilies Cervinae and Odocoileinae. The subfamily Odocoileinae, according to Bouvrain et al. (1989), includes also *Capreolus*, *Alces*, and *Rangifer*. The phylogenetic position of *Hydropotes* is regarded as uncertain, but closely related to Odocoileinae.

Vislobokova (1990) accepted with some modifications Simpson's (1945) classification and maintained the separation of plesiometacarpal and telemetacarpal cervids. According to Vislobokova (1990), the family Cervidae includes five modern subfamilies: Muntiacinae Pocock, 1923 (with tribes Dicrocerini Simpson, 1945 and Muntiacini Pocock, 1923); Cervinae Baird, 1857 (with tribes Pliocervini Khomenko, 1913, Cervini Gray, 1821, and Megacerini Viret, 1961); Odocoileinae; Alcinae; Hydropotinae; and three extinct subfamilies: Dremotheriinae Ginsburg et Heintz, 1966; Dromomerycinae Frick, 1937; and Lagomerycinae Pilgrim, 1941. Vislobokova (1990) suggests that the divergence of modern cervid subfamilies took place during the Early and Middle Miocene. According to Vislobokova (1990), the modern genus *Muntiacus*, together with the extinct *Eostyloceros*, *Paracervulus* and *Metacervulus*, take their origin from the Early and Middle Miocene Eurasian *Euprox*. The forerunner of Cervinae is also sought among the Middle Miocene Muntiacinae (genus *Dicrocerus*). Vislobokova (1990) included the tribe Pliocervini Khomenko, 1913 with genera *Cervavitus* Khomenko, 1913 and *Pliocervus* Hilzheimer, 1922 in the subfamily Cervinae, although she noted the uncertain systematic position of *Pliocervus*.

Di Stefano and Petronio (2002) challenged the taxonomic significance of the type of reduction of the lateral metacarpal bones in cervids, citing an earlier study by Lister and Chapman (1988) which found broad individual variation in the vestiges of lateral metacarpals in modern deer populations. Lister and Chapman (1988) attributed this variation to genetic bottleneck and inbreeding in British populations of fallow deer, and while they cautiously considered the possibility of parallel development of plesiometacarpality in Muntiacinae and Cervinae, they did not question the taxonomic and phylogenetic importance of plesiometacarpal and telemetacarpal conditions. In contrast, Di Stefano and Petronio (2002) included all antlered telemetacarpal and plesiometacarpal deer with the large complicated antlers in the subfamily Cervinae with six modern tribes (Neocervini Kalandadze and Rautian, 1992 [actually, the authorship belongs to Carette, 1922]); Odocoileini Pocock, 1923; Rangiferini Simpson, 1945; Alcini Simpson, 1945; Capreolini Brookes, 1828; Cervini Goldfuss, 1820) and two extinct tribes (Pliocervini Symeonidis, 1974 and Megacerini Viret, 1961).

Groves and Grubb (2011) revised their previous nomenclature scheme for cervids (Groves and Grubb, 1987), proposing to divide modern cervids into two subfamilies: Capreolinae Brookes, 1828 and Cervinae Goldfuss, 1820. Capreolinae, as defined by Groves and Grubb (1987), includes the tribe Rangiferini Brookes, 1828, which comprises the circumpolar genus *Rangifer* and all American telemetacarpal genera; the tribe Capreolini Brookes, 1828, which includes the genera *Capreolus* and *Hydropotes*; and the monotypic tribe Alceini Brookes, 1828. The subfamily Cervinae comprises the tribe Muntiacini Knottnerus-Meyer, 1907, which contains the modern genera *Muntiacus* and *Elaphodus*, and the tribe Cervini Goldfuss, 1820, which includes the genera *Cervus*, *Axis*, *Dama*, *Rucervus*, *Panolia*, and *Elaphurus* (Groves and Grubb, 2011). This classification of modern cervids is accepted in the present study.

The overview of various views on the systematics and classification of the family Cervidae reveals a lack of consensus regarding the classification of fossil and modern cervids. Disagreements on cervid systematics and phylogeny arise due to multiple unresolved questions, such as poorly understood evolutionary specializations within phylogenetic lineages, an incomplete fossil record of cervids, and superficial, inadequate, or inaccurate original descriptions of fossil cervid forms (Croitor, 2018b, 2020).

The misunderstood or poorly understood evolutionary significance of specific morphological characters provoked controversial and long-lasting debates on the phylogenetic positions of some genera and phyletic lineages.

Our understanding of the early paleontological record and evolution of the subfamily Capreolinae remains incomplete. Paleontological data and their interpretations have not provided a clear picture of the early evolutionary stages and phylogenetic relationships of telemetacarpal deer. Phylogenetic relationships within this group are not well understood, and the extreme specialization of the modern representatives of Capreolinae, which belong to a heavily depleted evolutionary branch of cervids, has been noted by Geist (1998). Most of the modern Capreolinae, or telemetacarpal deer, represent a relatively recent and successful evolutionary radiation of cervids in the New World. In the Old World, there are only three telemetacarpal genera with four species (*Capreolus capreolus*, *C. pygargus*, *Alces alces*, *Hydropothes inermis*), while *Rangifer tarandus* is an extremely specialized cervid with circumpolar distribution (Lydekker, 1898; Flerov, 1952; Geist, 1998). The first known members of the genera *Alces*, *Capreolus*, and *Rangifer*, already exhibiting the specialized features characteristic of these groups, appeared in the Pliocene and Early Pleistocene of Asia (Vislobokova et al., 1995; Webb, 2000; Bondarev et al., 2017). The extreme evolutionary specializations of the Capreolinae and the absence of transitional forms have resulted in long-lasting debates on the systematic position and phylogenetic relationships of most of the Old World telemetacarpal deer (with the exception of *Rangifer*).

Pavlodaria orlovi (Flerov, 1950) from the Late Miocene of Eastern Kazakhstan is a unique deer with completely divided vomer nasal chambers, like New World telemetacarpal deer

(Vislobokova, 1980). Vislobokova (1980) suggests that *Pavlodaria orlovi* still maintains holometacarpal limbs but belongs to the tribe Odocoileini. Therefore, the subfamily Capreolinae (Odocoileinae according to Vislobokova, 1990) is redefined as a taxonomic group that includes both telemetacarpal and primitive holometacarpal forms. Modern molecular genetic studies have confirmed the monophyly of all telemetacarpal deer, but the adequacy of systematic models based on morphology has been called into question (Douzery and Randi, 1997; Polzein and Strobeck, 1998; Randi et al., 1998; Gilbert et al., 2006). However, analysis of bony labyrinth morphology of modern and fossil deer has produced results consistent with the phylogenetic relationships between cervids, confirming the monophyly of the Old World telemetacarpal deer (Mennecart et al., 2017).

Procapreolus is the extinct genus from the Late Miocene to Pliocene of Eurasia that was invariably approached to modern telemetacarpal deer (Dawkins, 1878; Schlosser, 1924; Korotkevich, 1970; Vislobokova and Kalmykov, 1994; Vislobokova, 1990; Webb, 2000). Valli (2010) confirmed the subfamily Capreolinae's belonging to *Procapreolus* by providing a detailed description of the basicranial morphology of *P. cusanus*. *Pavlodaria orlovi* (Flerov, 1950) from the Late Miocene of Eastern Kazakhstan is another extinct deer that belongs to the subfamily Capreolinae, with its nasal chambers completely divided by the vomer, as is typical in the New World telemetacarpal deer (Vislobokova, 1980). According to Vislobokova (1980), *P. orlovi*, placed in the tribe Odocoileini, still maintains holometacarpal limbs. As a result, Vislobokova (1990) redefined the subfamily Capreolinae as a taxonomic group that includes both telemetacarpal and holometacarpal forms.

For a long time, *Hydropotes inermis*, which lacks antlers, was considered the most primitive cervid species, representing an initial stage in the evolutionary development of the family Cervidae. It was placed in the subfamily Hydropotinae, which was distinct from all other antlered deer species (Flerov, 1952; Azzaroli, 1953; Groves and Grubb, 1987; Vislobokova, 1990; Danilkin, 1999; Grubb, 2000; Di Stefano and Petronio, 2002).

The elk group, consisting of the genera *Alces* and *Cervalces*, presents a challenge for cervid classification due to unresolved phylogenetic relationships. The unique morphological features of elk antlers and skulls make it difficult to determine their clear affinities with other cervid groups. As a result, all elks were originally placed in the separate subfamily Alcinae (Azzaroli, 1953; Vislobokova, 1990; Boeskorov, 2001). However, Flerov (1952) and Sokolov (1959) included *Alces* in the subfamily Cervinae, while Bouvrain et al. (1989) placed it within the subfamily Odocoileinae. Geist (1998) suggested that the elk (or moose) diverged from other New World deer in the late Tertiary.

Azzaroli (1953) included *Capreolus* in the subfamily Capreolinae and suggested a close relationship between Capreolinae and Alcinae based on the affinity in dental morphology. In contrast, Flerov (1952) regarded *Capreolus* as a primitive cervid, close to the muntjac-like evolutionary stage, and included this genus in the subfamily Cervinae. Sokolov (1959), Czyżewska (1968), and Di Stefano and Petronio (2002) followed Flerov's point of view. However, roe deer (together with Mio-Pliocene *Procapreolus*) are more often grouped with the American deer in the subfamily Capreolinae (= Odocoileinae) (Simpson, 1945; Korotkevich, 1988; Bouvrain et al., 1989; Vislobokova, 1990; Vislobokova and Kalmykov, 1994; Danilkin, 1999; Grubb, 2000).

The phylogenetic relationships and origin of Eurasian plesiometacarpal deer (cervines) are still not well established and require critical reconsideration. While the separation of muntjacs and large plesiometacarpal deer with complicated antlers at the subfamily level or even in different families has been traditionally accepted (Khomenko, 1913; Simpson, 1945; Flerov, 1952; Azzaroli, 1953; Korotkevich, 1988; Groves and Grubb, 1990; Vislobokova, 1990; Di Stefano and Petronio, 2002), the inclusion of all plesiometacarpal deer in the single subfamily Cervinae, as suggested by Brooke (1878), has often been disregarded and remained a marginal point of view.

Cervavitus novorossiae, supposedly holometacarpal, from the Late Miocene of southeastern Europe is often regarded as the most primitive member of the Cervinae, based on the old hypothesis of Khomenko (1913) regarding the mixture of muntiacine and cervine characters in the cranial morphology of *Cervavitus*. However, the phylogenetic relationships among the fossil cervines in most cases remain unclear or poorly supported by arguments (Croitor, 2021). Often, the phylogenetic interpretations of fossil cervid forms are based on a limited set of arbitrarily selected or available characters, such as antler and cranial morphology (Vislobokova, 1990), antler shape (Azzaroli and Mazza, 1992; Di Stefano and Petronio, 2002), postcranial morphology (Pfeiffer, 1999), or general eco-morphology (Flerov, 1952).

The main taxonomic challenge in classifying the subfamily Cervinae arises from the relatively uniform craniodental morphology that makes it difficult to distinguish between genera. Some authors, such as Flerov (1952), have a broad interpretation of the genus *Cervus*, which includes the rusa deer, the axis deer, and the fallow deer. In contrast, Pocock (1942, 1943a, b, c) proposes the opposite viewpoint and recognizes valid status for several genera within Cervinae, including *Cervus*, *Axis*, *Hyelaphus*, *Panolia*, *Rucervus*, and *Przewalskium*.

The relationship between modern and fossil cervid taxa has been poorly studied and, for the most part, remains speculative. Despite some attempts to trace a link between fossil forms of cervids and modern genera, there is a significant taxonomic gap between them (Flerov, 1952; Di Stefano and Petronio, 2002).

Antlers are traditionally considered the primary source of diagnostic morphological characters used in the description of fossil deer species and genera and, therefore, play a crucial role in phylogenetic studies (Azzaroli and Mazza, 1992). This is because antlers are the most specific, morphologically well-defined, and expressive remains of fossil cervids, which are relatively abundant in the fossil record. The shape of antlers is closely linked to the social and reproductive behavior of deer (Geist, 1998). Therefore, antlers should be considered a reliable source of diagnostic characters for species description, despite the well-known individual, geographical, ontogenetic, and pathological variability of antler morphology (Heintz, 1970).

In contrast, neontological taxonomy of mammals, including cervids, relies primarily on skull morphology, unlike palaeontological taxonomy. As a result, the morphological criteria for fossil and modern cervid taxa at the species and genus levels are often based on different characteristics that are challenging to compare, leading to methodological incompatibility between paleontological and neontological cervid taxonomy. As Simpson (1945) correctly pointed out, the classification of living cervids is relatively easy to arrange; nonetheless, despite the great abundance of fossil forms, they shed little light on the phylogenetic interrelationships of the modern deer.

Over the last two decades, the analysis of mitochondrial and nuclear DNA sequences has significantly advanced the understanding of modern cervid phylogeny. Molecular analysis is a valuable tool for interpreting data on fossil deer. Research shows that the divergence between plesiometacarpal and telemetacarpal deer is a major basal event in modern cervid phylogeny, occurring in the Late Miocene (8.7-10.4 Ma according to Douzery and Randy, 1997; 7.8-7.9 Ma according to Gilbert et al., 2006; or 10.7-11.5 Ma according to Hassanin et al., 2012). Unexpectedly, a close phylogenetic relationship between *Capreolus* and *Hydropotes* was discovered. All Old World telemetacarpal cervids, including *Alces*, *Capreolus*, *Rangifer*, and *Hydropotes*, together with the New Old deer, form a monophyletic clade of telemetacarpal cervids (Douzery and Randy, 1997; Randi et al., 1998; Pitra et al., 2004; Gilbert et al., 2006). The clade *Capreolini-Hydropotini-Alcini* emerged during the Middle Miocene between 15.6 and 16.8 Ma ago and remains quite distant from the New World tribes of Capreolinae (Odocoileini and Rangiferini) (Randi et al., 1998). Hassanin et al. (2012) report a more recent dichotomy of the Eurasian (including *Alces*) and American Capreolinae (8.7-9.6 Ma).

The close phylogenetic association between the Cervinae and the Muntiacinae is strongly supported by molecular analysis (Miyamoto et al., 1990; Pitra et al., 2004; Gilbert et al., 2006). This result was somewhat unexpected, as the subfamily Muntiacinae was traditionally placed at the base of the cervid phylogenetic tree, along with the extinct muntjac-like primitive cervids

(Simpson, 1945; Flerov, 1952; Vislobokova, 1990). However, the close relationship between modern muntjacs and cervines (subfamily Cervinae) is consistent with most of the available morphological and biochemical data (Brooke, 1878; Bouvrain et al., 1989). Thus, the plesiometacarpal condition among the modern cervids evolved only once through the reduction of lateral metacarpals. This new insight into cervid phylogeny highlights the taxonomical significance of the type of reduction of lateral metacarpals and supports the natural grouping of modern plesiometacarpal cervids (Randi et al., 1998).

Modern molecular genetic studies have also confirmed the monophyly of all telemetacarpal deer, but have raised questions about the adequacy of systematic models based solely on morphology (Douzery and Randi, 1997; Polzein and Strobeck, 1998; Randi et al., 1998; Gilbert et al., 2006). However, analysis of the bony labyrinth morphology of modern and fossil deer has produced relatively reliable results on the phylogenetic relationships between cervids and has confirmed the monophyly of the Old World telemetacarpal deer (Mennecart et al., 2017). The morphological analysis of the bony labyrinth has yielded interesting results that have opened up new perspectives for the phylogenetic study of fossil cervids. Mennecart et al. (2017) have confirmed the monophyly of the Old World telemetacarpal deer (subfamily Capreolinae) and identified *Euprox furcatus* as a member of the subfamily Cervinae, which diverged very early from the main cervine phylogenetic branch. They also found that modern *Muntiacus* belongs to the zoogeographically more restricted South-East Asian radiation together with large cervines. The methodology developed and used by Mennecart et al. (2017) is of great interest, as it permits the inclusion of both modern and fossil forms in phylogenetic studies.

The radiation of advanced plesiometacarpal Old World deer likely began around the Miocene/Pliocene boundary (3.3-7.1 Ma), with the final diversification within Cervinae occurring during the Early Pleistocene (0.4-2.5 Ma), leading to the evolution of modern subspecies of *Cervus elaphus* (Douzery and Randy, 1997). Pitra et al. (2004) found that *Axis axis*, *Rucervus schomburgki*, and *Rucervus duvaucelii* diverged early from the main phylogenetic stock of Cervinae. *Przewalskium albirostris*, the white-lipped deer, is a sister species to a wapiti/shou/sika clade within the genus *Cervus* (Pitra et al., 2004). *Dama*, the only modern cervid genus not found in Southeast Asia, diverged quite early from *Cervus* and allied cervines in Southeastern Asia, during the Early Pliocene around 3.0 Ma (Pitra et al., 2004; Gilbert et al., 2006). Molecular phylogeny analysis has also revealed the surprising importance of hybridization in the evolution and origin of modern cervid species. At least two such evolutionary events are recorded among modern cervids: the non-monophyletic origin of the red deer/wapiti group, previously regarded as a single species (*Cervus elaphus*), and the origin of the enigmatic species *Elaphurus davidianus*.

The genus *Elaphurus* resulted from the hybridization of ♀*Panolia eldii* (or a very similar form) and ♂*Cervus canadensis*, and is therefore closely related to the phylogenetic stock of *Cervus* and related forms (Meijaard and Groves, 2004; Pitra et al., 2004).

New evidence suggests that the genus *Muntiacus*, which was once thought to be a primitive precursor of all modern deer, is actually a fairly specialized taxon that belongs to the modern evolutionary radiation of the subfamily Cervinae. The plesiometacarpal condition in *Muntiacus* has attained the highest evolutionary degree. Nevertheless, *Muntiacus* still bears some resemblance to the hypothesized ancestral type of Cervidae, which was a small-sized, cryptic, holometacarpal forest inhabitant with large tusks, long pedicles, and small, simple antlers (Flerov, 1952; Czyżewska, 1968; Janis and Scott, 1987; Vislobokova, 1990; Geist, 1998). The majority of Miocene Cervidae, including the earliest representatives of Cervinae (such as "*Cervavitus*" from the Late Tertiary of China) and Capreolinae (such as *Cervavitus*, *Pliocervus*, and *Procapreolus* from Western Eurasia), had well-developed enlarged upper canines (Vislobokova, 1990; Gentry et al., 1999).

The results of molecular phylogenetic studies on cervids have advanced our understanding of the systematics of modern deer and prompted a reevaluation of the taxonomic value of certain characteristics of modern cervid forms, such as antler complexity and other exosomatic features, which appear to be influenced by lifestyle factors related to climate (Groves, 2005). These new insights into cervid evolution also provide an excellent opportunity for revising the taxonomic criteria used to classify fossil species and for developing a new perspective on the phylogenetic and evolutionary relationships among fossil and modern cervid forms and clades.

Previous attempts to reconcile fossil cervid records with new molecular phylogeny data have been controversial, with the most contentious issues centering around the identification of the ancestral form of modern large antlered cervines. Pitra et al. (2004), following di Stefano and Petronio (2002), consider the Late Miocene holometacarpal *Cervavitus novorossiae* to be the most primitive member of the Cervinae. However, the reconstruction of the cervid ancestral morphotype as a large open landscape dweller with a strong sexual dimorphism, three-pointed antlers, and missing upper canines proposed by Gilbert et al. (2006) is highly contentious. This daring hypothesis conflicts with paleontological and biological data (Vislobokova, 1990; Geist, 1998; Croitor and Stefaniak, 2009).

Firstly, the fossil record provides clear evidence that the ancestral type of Cervidae was a small-sized, cryptic, holometacarpal forest inhabitant with large tusks, long pedicles, and small simple antlers (Flerov, 1952; Czyżewska, 1968; Janis and Scott, 1987; Vislobokova, 1990; Rössner, 1995; Geist, 1998). The enlarged upper canines are well-developed in the majority of

Miocene Cervidae, including the earliest representatives of Cervinae (apparently, "*Cervavitus*" from China) and Capreolinae (*Procapreolus* from Western Eurasia) (Vislobokova, 1990; Gentry et al., 1999). Furthermore, the ancestral morphotype proposed by Gilbert et al. (2006) cannot explain the presence of vestigial preorbital fossae in almost all Cervidae, regardless of ecological adaptations. It is worth noting that preorbital fossae serve the function of chemical communication in forest deer and achieve the strongest development in Muntiacinae, as well as in the most primitive fossil Capreolinae (*Procapreolus*) and primitive fossil and modern Cervinae (*Hyelaphus*).

The available paleontological data and their interpretations did not clarify the early evolution stages and phylogenetic relationships of the telemetacarpal deer. The earliest representatives of *Alces*, *Capreolus*, and *Rangifer* appear in the Pliocene and Early Pleistocene of Asia and already show specialized features characteristic of those genera (Vislobokova et al., 1995; Webb, 2000; Bondarev et al., 2017). *Procapreolus* is the extinct genus from the Late Miocene to Pliocene of Eurasia that was invariably approached to modern telemetacarpal deer (Dawkins, 1878; Schlosser, 1924; Korotkevich, 1970; Vislobokova and Kalmykov, 1994; Vislobokova, 1990; Webb, 2000). Valli (2010) confirmed the belonging of *Procapreolus* to the subfamily Capreolinae, providing a detailed description of the basicranial morphology of *P. cusanus*. *Pavlodaria orlovi* (Flerov, 1950) from the Late Miocene of Eastern Kazakhstan is a peculiar deer characterized by the completely divided vomer nasal chambers as New World telemetacarpal deer (Vislobokova, 1980). According to Vislobokova (1980), *P. orlovi* still maintains holometacarpal limbs but belongs to the tribe Odocoileini. Therefore, the subfamily Capreolinae (Odocoileinae *fide* Vislobokova, 1990) is redefined as a taxonomical group that includes telemetacarpal and primitive holometacarpal forms.

1.2. Main issues in cervid systematics and taxonomy

The validity of Pliocervinae. Most holometacarpal (and supposedly holocarpal) deer are grouped within the poorly defined subfamily Pliocervinae, often considered a tribe within the subfamily Cervinae (Simpson, 1945; Czyżewska, 1968; Vislobokova, 1990; Azanza, 2000; Grubb, 2000; Di Stefano and Petronio, 2002). Aleksejev (1913, 1915) was the first to describe the holometacarpal limb condition in his *Procervus variabilis* from the Late Miocene of South Ukraine. Khomenko (1913) included Aleksejev's species in the subfamily Pliocervinae, which was created to describe the transitional evolutionary stage between primitive muntiacines and advanced cervines of the modern type. Khomenko's *Pliocervinae* included new genera and species, such as *Cervocerus novorossiae*, *Cervavitus tarakliensis*, and *Damacerus bessarabiae*, as well as previously described species such as *Cervus matheroni* Gervais, *Dremotherium pentelici* Gaudry, and *Cervavitus speciosus* Schlosser (Khomenko, 1913). The subfamily Pliocervinae was accepted by Zdansky (1925), while Simpson (1945) regarded Pliocervinae Khomenko, 1913 as a synonym of Cervinae Baird, 1857.

In 1968, Czyżewska revised the taxonomy of the subfamily Pliocervinae, downgrading it to the tribe Pliocervini within Cervinae and recognizing a single genus, *Cervavitus* Khomenko, 1914. Czyżewska also proposed that the Asian "Pliocervini" may be the ancestors of *Axis* and *Cervus*. However, Czyżewska regarded *Pliocervus* Hilzheimer, 1922 as a genus *incertae sedis* and did not include it in *Pliocervini*. Therefore, the *Pliocervini* sensu Czyżewska is not based on *Pliocervus* Hilzheimer.

Petronio et al. (2007) incorrectly attributed the authorship of the tribe Pliocervini to Czyżewska, 1968. In contrast, Korotkevich (1988) and Vislobokova (1990) included both *Pliocervus* and *Cervavitus* in the tribe *Pliocervini* Khomenko, 1913 within the subfamily Cervinae Baird, 1857.

Grubb (2000) demonstrated that the subfamily name Pliocervinae Khomenko, 1913 is not based on a valid genus-group name, and therefore it is not an available taxon according to Article 29 of the ICZN. However, in 1974 Symeonidis proposed the subfamily Pliocervinae with *Pliocervus* and *Cervavitus*, which is based on *Pliocervus* Hilzheimer, 1922 and is therefore an available family-group name. Grubb (2000) recognized *Pliocervus* in the subfamily Pliocervinae Symeonidis 1974, together with *Cervavitus*. Meanwhile, McKenna and Bell (1997) applied the tribe Pliocervini Symeonidis, 1974 within the subfamily Cervinae with the genera *Cervavitus* and *Pliocervus*.

The genus name *Cervocerus* Khomenko, 1913 (previously known as *Cervavitus* Khomenko, 1913) is traditionally used to describe medium to small-sized cervids with relatively short three-pointed antlers and long pedicles from the Late Tertiary and Quaternary periods of China and Central Asia. Up to eight species or subspecies have been identified, along with up to three species from the Late Miocene to Pliocene of Europe (Aubekerova, 1974; Dong, 2011; Wang and Zhang, 2014; Vislobokova, 1990).

However, the classification of Chinese and Central Asian forms as belonging to *Cervocerus*/*Cervavitus* is disputed (Azzaroli, 1953; Czyżewska, 1968; Vislobokova, 1990; Petronio et al., 2007)

The subfamily Pliocervinae (Grubb, 2000), which has been a keystone systematic group in the evolutionary and phylogenetic models of plesiometacarpal deer (Khomenko, 1913; Flerov, 1950, 1952; Czyżewska, 1968; Vislobokova, 1990; Di Stefano and Petronio, 2002), is questionable. It is important to note that the systematic position of *Pliocervus matheroni*, the type species of Pliocervinae, remains unclear (Czyżewska, 1968; Vislobokova, 1990).

This study aims to assess the taxonomic weight and systematic importance of craniodental, antler, and some selected postcranial characters of cervids. The subfamily Capreolinae is of particular interest for this study, as its highly specialized representatives are characterized by a variety of combinations of cranial, dental, and antler characters (Croitor and Stefaniak, 2009). Reassessing diagnostic craniodental and antler characters will provide a new perspective on the systematic position and phylogenetic relationships of Late Miocene European "Pliocervinae." This subfamily will be subjected to a taxonomic revision and morphological redescriptions (Croitor, 2021)

The systematical position of *Pliocervus*. The systematic position of *Pliocervus matheroni* is a matter of debate, and no convincing arguments have been presented thus far. In his original description, Gervais (1852) considered *Cervus* (*Axis*) *matheroni* to be an intermediate form between roe deer and primitive cervine deer. Later, Gaudry (1873) noticed a certain affinity between the antler shape of *C. matheroni* and South American *Ozotoceros bezoarticus* (= *Cervus campestris*: Grubb, 2000). Dawkins (1878) considered *C. matheroni* to be similar to modern roe deer and included it in the group of roe-like deer, or Capreoli. This viewpoint was supported by Lydekker (1885) and Trouessart (1899), who included *C. matheroni* in the genus *Capreolus*.

Khomenko (1913) endorsed Gervais' (1852) initial presumption about the transitional evolutionary position of the deer from Mont Luberon. According to Khomenko (1913), the deer from Mont Luberon, together with the Late Miocene cervids from Bessarabia, represents the evolutionary link between primitive muntjacs and crown deer of the modern type. Subsequent authors (Czyżewska, 1968; Korotkevich, 1970; Vislobokova, 1990; Azanza, 2000) regarded *Pliocervus matheroni* as a primitive representative of the subfamily Cervinae with unclear phylogenetic relationships.

Korotkevich (1970) noticed a similar pattern of antler construction in *Pliocervus matheroni* and *Cervavitus orlovi* Flerov, 1950, from the "*Hipparion* fauna" of Pavlodar (North-East Kazakhstan). Later, Vislobokova (1980) created a new genus, *Pavlodaria*, for *Cervavitus orlovi*, which is considered an archaic deer of the subfamily Capreolinae (= Neocervinae Carette, 1922) due to the set of important cranial characters, such as the bone septum completely dividing the nasal choanae and the specific morphology of post-glenoid foramen that is not surrounded by squamosal bone and is bordered in its posteromedial part by the petrous bone, which is characteristic of Capreolinae. The systematic position of *Pliocervus*, according to Vislobokova (1990), remained uncertain. Although Vislobokova (1980, 1990) placed *Pliocervus* together with

Cervavitus in the tribe Pliocervini Khomenko, 1913, of the subfamily Cervinae Baird, 1857, she notes a certain affinity of its antler morphology with *Pavlodaria* and *Odocoileus*.

The imperfect definition of *Pliocervus* and its type species has caused confusion in taxonomy. Several ruminant species are poorly known and misunderstood, and have been included in *Pliocervus*. One such species comes from the Late Miocene of Pikermi (Greece, MN12). Gaudry (1865) reported a braincase without cranial appendages and lower mandibles with primitive cervid-like dental morphology from Pikermi as the new species *Dremotherium pentelici*, which was suggested as a transitional link between mouse-deer and other ruminants. Dames (1883) proposed a new species, *Cervus pentelici*, based on well-preserved three-pointed antlers from Pikermi and assumed its close relationship with *Cervus matheroni*. It is important to note that *C. pentelici* Dames, 1883 is not a homonym of *Dremotherium pentelici* Gaudry, 1865.

Melentis (1968) associated *Dremotherium pentelici* with the antlers of *C. pentelici* and included Gaudry's species in the genus *Pliocervus*, therefore proposing a new species and genus combination, *Pliocervus pentelici* (Gaudry, 1865). However, the inclusion of *Dremotherium pentelici* in the genus *Pliocervus* was doubted by Gentry et al. (1999) and Croitor (2014). Azanza (1995) indicated that three forms of ruminants were finally grouped under the name *Pliocervus* pentelici: a bovid braincase with inflated large bullae tympani; a mandible of small-sized cervid; and a larger deer represented by mandible fragments described by Gaudry (1865) as *Dremotherium sp*. and antlers described by Dames (1883) as *C. pentelici*. Azanza (1995) restricted the original name *Dremotherium pentelici* to the mandibles of the smaller deer.

My revision of Gaudry's collection stored in the National Museum of Natural History in Paris confirms Azanza's (1995) suggestion. The braincase PIK2020 (MNHN, Paris) belongs to a bovid. The specimen is not lost, as reported by Azanza (1995) and Gentry (2005). The collection label of this specimen defines it as "*Gazella brevicornis* cf. *capricornis*/*deperdita*?".

The hemimandibles PIK2034a and PIK2034b belong to a very small deer similar in size to modern *Muntiacus reevesi* and *Hydropotes inermis*. These specimens are characterized by a primitive P_4 and a very weak *Palaeomeryx* fold. The systematic position of this deer is not yet clear. Kostopoulos (2006) identified the small cervid mandibles from Pikermi as belonging to the genus Lucentia Azanza and Montoya, 1995, while Azanza et al. (2013) suggest that the size of smaller teeth from Pikermi is more similar to *Cervavitulus mimus*.

The antlers from Pikermi are three-pointed, thin, and have a high position of the first ramification (Dames, 1883; Melentis, 1968) and belong to *Procapreolus* (Croitor, 2018b). Azanza (1995) proposed a new species name, *Pliocervus graecus*, for the sample from Maramena and the antlers from Pikermi, following the misleading and confusing definition of *Pliocervus*. The antlers of *P. graecus* are very similar to those of *P. flerovi* from the Late Miocene of Ukraine (Croitor, 2018b).

Pliocervus kutchurganicus Korotkevich, 1965 is based on a series of antlers of different ontogenetic stages. The holotype of this species is a basal fragment of a shed antler Nr. 37-1 (IZU) from the early Pliocene deposits of the Kuchurgan River (Ukraine). Korotkevich (1970) assigned several fragments of lower mandibles with molarized P_4 and molars lacking the *Palaeomeryx* fold to *P. kutchurganicus*, and pointed out a set of characteristics that distinguish it from *Procapreolus*, including the more robust antler with a comparatively low position of the first tine, the presence of an anterior groove on the antler, the short pedicle, and the lack of *Palaeomeryx* fold.

The ontogenetic development of antlers was suggested by Korotkevich (1970) as an important character distinguishing *Pliocervus* and *Procapreolus*. According to the cited author, in *Pliocervus* the first tine develops before the distal bifurcation, while in *Procapreolus* the distal bifurcation appears before the first tine. However, this type of juvenile antler can also be seen in *Procapreolus* (Korotkevich, 1970: p. 116, fig. 43d; 1988: p. 68, fig. 33b), and even in modern *Capreolus capreolus* (Croitor and Stefaniak, 2009). Thus, the difference in ontogenetic development of antlers between *Pliocervus kutchurganicus* and *Procapreolus* may not be a good argument. Since the diagnostic characters of *P. kutchurganicus* established by Korotkevich (1970) fall within the morphological variation range of *P. moldavicus* from Węże-1, we consider that *P. kutchurganicus* is a junior synonym of *P. moldavicus* (Croitor, 2018b).

Pliocervus karabastuzikus Abdrakhmanova, 1974 is another species that is poorly known, as it is based solely on a two-tined antler from Eastern Kazakhstan that does not exhibit any clear similarity to *Pliocervus matheroni*. *Pliocervus turoliensis*, a new species described by Azanza (2000), is also based on fragments of antlers and pedicles that are very poor in quality and do not display any clear diagnostic features of *Pliocervus*.

The dentition, antlers, and orientation of pedicles of *Pliocervus matheroni* show main morphological characteristics similar to those of Late Miocene *Pavlodaria orlovi* from the Hipparion fauna of Pavlodar, Kazakhstan. Korotkevich (1970) has reasonably suggested a similarity in antler construction between *Pavlodaria orlovi* (= *Cervavitus orlovi* according to Korotkevich 1970, page 62) and *Pliocervus matheroni*. The deer from Pavlodar is distinguished only by more advanced morphology of the molarized P_4 and flattened antlers. Taking into consideration the basicranial morphology, Vislobokova (1980) regards the cervid from Kazakhstan as the earliest representative of the New World cervid lineage. Therefore, the genera *Pliocervus* Hilzheimer, 1922 and *Pavlodaria* Vislobokova, 1980 are likely very close or even synonymous, and this observation is important since it implies the belonging of *Pliocervus* to the subfamily Capreolinae. If we keep the genus *Pavlodaria*, the genus *Pliocervus* should be restricted to the type species *Pliocervus matheroni*.

Azanza (2000) cites the divergent pedicles in *Pliocervus* as a differential diagnostic character that contrasts with the parallel pedicles of *Procapreolus*. However, this statement is erroneous because the type material from Cucuron shows a parallel orientation of pedicles in *Pliocervus matheroni*, while the pedicles of *Procapreolus moldavicus* from Weże are rather divergent, as in modern *Odocoileus*.

Cervavus rutimeyeri Schlosser, 1903 from the Late Tertiary of Mongolia and China exhibits a striking similarity in antler morphology to *Pliocervus matheroni*. *C. rutimeyeri* shares with *P. matheroni* the simple morphology of P_4 but lacks the *Palaeomeryx* fold that is present in *P. matheroni* (Schlosser, 1903, 1924). This indicates a Late Miocene radiation of cervids in North Asia that includes *Pliocervus matheroni*, *Pavlodaria orlovi*, and *Cervavus rutimeyeri*, with the most advanced form being *P. orlovi* with flattened antlers and molarized P_4 in Central Asia. Although the genera *Pliocervus*, *Pavlodaria*, and *Cervavus* are maintained in this work, the distinguishing characteristics of those forms are typically used to differentiate between cervid species.

The taxonomical status of Megalocerotini Brookes, 1828. Viret (1961) proposed that the giant deer be placed in a separate tribe, Megacerini, based on the genus *Megaceros* Owen, 1844. This point of view has been accepted and defended by Vislobokova (1990, 2009, 2012a, 2012b, 2013) and di Stefano and Petronio (2002). However, Lister (1987) argued that the genus name *Megaloceros* Brookes, 1828 should have priority over *Megaceros* Owen, 1844, and this viewpoint has been widely accepted. Later, Lister (1994) substituted Megacerini Viret with Megalocerini and suggested that *Dama* might be the only surviving genus of this tribe. Abbazzi and Masini (1996) quoted Lister's tribe name as Megalocerini Viret, 1961.

While Vislobokova (2009) accepts the genus name *Megaloceros*, she continues to use the tribe name Megacerini based on *Megaceros*. However, Grubb (2000) has pointed out that Megacerini Viret, 1961 is a junior synonym of Megalocerotinae Brookes, 1828, and that the correct name for the tribe should be Megalocerotini Brookes, 1828. According to Grubb (2000), the genera *Praemegaceros*, *Megaceroides*, *Megaloceros*, and *Sinomegaceros* belong to the tribe Cervini Goldfuss, 1820, and in this case, Megalocerotini Brookes, 1828 should be regarded as a synonym of Cervini Goldfuss, 1820

The taxonomic unit of the tribe Megacerini Viret, 1961 quickly emerged as a grouping for large Old World fossil cervids with unclear phylogenetic relationships and their assumed smaller relatives. Some researchers accepted this taxonomic group in its broad sense (Czyżewska, 1968;

Lister, 1987; Vislobokova, 1990, 2009; Di Stefano and Petronio, 2002). Vislobokova (1990, 2009, 2012, 2013) identified the giant deer as a distinct and well-defined phylogenetic group of cervines, and included up to 11 genera from Eurasia and Mediterranean islands with a geological range from the Late Miocene to the Early Holocene within the tribe Megacerini.

Vislobokova (1990, 2009, 2012, 2013) identified eight genera belonging to the tribe of giant deer: *Megaloceros*, *Praemegaceros*, *Sinomegaceros*, *Praesinomegaceros*, *Praedama*, *Orchonoceros*, *Arvernoceros*, and *Neomegaloceros*. However, this list represents an eclectic group, including forms from various phylogenetic stocks, as well as poorly understood cervid forms, like *Neomegaloceros gracilis* (Croitor, 2006a, 2016).

Radulescu and Samson (1967) and Azzaroli and Mazza (1992, 1993) suggest that Eucladoceros may be a primitive forerunner of *Praemegaceros*, citing similarities in the general construction of antlers. Furthermore, *Praemegaceros* shares essential cranial characteristics and antler morphology with *Eucladoceros*, and a direct phylogenetic relationship between the two genera is accepted by many authors (Radulesco and Samson, 1967; Azzaroli, 1979; Azzaroli and Mazza, 1993; Abbazzi, 2004; Croitor, 2006a, 2014).

Earlier, Croitor (1997) suggested grouping *Praemegaceros*, *Eucladoceros*, and *Orchonoceros* together in the tribe *Eucladocerini*. However, based on current knowledge, this taxon is now considered a synonym of Cervini Goldfuss, 1820.

The proposed close phylogenetic relationship between *Megaloceros* and *Praedama* is based on a single morphological feature: the flattened basal tine (Azzaroli, 1953; Vislobokova, 1990; van der Made and Tong, 2008). However, several morphological characteristics of *Praedama* require further investigation before its close relationship to giant deer can be confirmed. While the flattened proximal part of the basal tine in *Praedama savini* (as the complete basal tines are unknown) may support the hypothesis of a close relationship between *Megaloceros* and *Praedama*, it is also a characteristic feature of *Eucladoceros dicranios* (Croitor, 2018b). Additionally, the dental and mandibular remains of *Praedama* from Cueva Victoria do not show any evidence of cingulum in upper molars, nor any clearly expressed mandibular pachyostosis (van der Made, 2014). The skull morphology of *Praedama* is currently unknown, and well-founded arguments on the phylogenetic relationships of this genus are missing. Further craniological material may provide a clearer understanding of the systematic position and phylogenetic relationships of *Praedama*.

The proposed tribe Megalocerotini (= Megacerini) *sensu lato* as suggested by Vislobokova (1990, 2009, 2013) is a polyphyletic group that includes lineages not only from the subfamily Cervini but also from the subfamily Capreolini. Most of the cervid forms included in this tribe by

Vislobokova represent a unique eco-evolutionary type of open landscape giants with large antlers (*Megaloceros*, *Praemegaceros*) that have no modern analogues, as well as forest/woodland giants with smaller antlers (*Sinomegaceros*) that are similar to the eco-evolutionary type of modern *Alces alces*.

To accurately define the tribe Megalocerotini Brookes, 1828 *sensu stricto*, it should be limited to the genera *Megaloceros*, *Megaceroides*, and *Dama*. However, a reliable differential diagnosis of the tribe is difficult in this case since the representatives of those three genera are highly specialized. Grubb (2000) grouped all Old World deer with small or missing upper canines and large complicated antlers into the single tribe Cervini Goldfuss, 1820. The tribe Cervini Goldfuss, 1820 could possibly be restricted to the phylogenetic branch of *Cervus* and related genera (or subgenera) *Hyelaphus*, *Rusa*, *Panolia*, and *Przewalskium*, since this cervid group shares similar cranial and dental characteristics, such as the presence of small upper canines and a narrow triangular basioccipital. Additionally, genetic analysis revealed their monophyly (Pitra et al., 2004).

The phylogenetic position of *Megaloceros*, commonly known as the giant deer, has been the subject of extensive debate among researchers. Several hypotheses have been proposed over the years, and various studies have produced conflicting results.

Early researchers, such as Owen (1846) and Reynolds (1929), proposed that *Megaloceros* was closely related to the modern fallow deer, *Dama dama*. This proposition was supported by some molecular phylogenetic studies, which revealed that the fallow deer is the extant cervid species most closely related to *Megaloceros*, despite an evolutionary divergence that occurred between 4-5 million years ago (Lister et al., 2005), or potentially even as far back as 10.7 million years ago (Hughes et al., 2006).

In contrast, Lönnberg (1906) suggested that *Megaloceros* was related to *Rangifer*, or the reindeer, due to a unique cranial characteristic that both species share - an ossified vomer that divides the posterior nares into two separate passages. However, this hypothesis is not widely supported in the literature.

Heintz (1970) proposed that *Rucervus* (*Arvernoceros*) *ardei*, a fossil deer species from the Pliocene or Perrier-Etouaires in France, was a likely forerunner to *Megaloceros*. This hypothesis was based on shared morphological features between the two species, such as the cingulum in upper molars, the accessory prong on the somewhat flattened basal tine, and the development of distal palmation.

Despite these proposals, the systematic position of *Megaloceros* remains uncertain, and further research is required to elucidate its evolutionary relationships with other fossil deer species.

The taxonomical problem of *Megaceroides* and *Praemegaceros*. The nomenclature of the "*verticornis* group" has long been a subject of debate. Kahlke (1956) proposed the creation of a new genus, *Orthogonoceros*, with *Cervus verticornis* Dawkins, 1872 as the type species. Subsequently, Kahlke (1965) designated *Praemegaceros* Portis, 1920 as the genus name, with *Cervus dawkinsi* Newton, 1882 from the Middle Pleistocene of England as the type species. Ambrosetti (1967) proposed *Megaceroides* Joleaud, 1914 as an alternative genus name for the arbitrary "*verticornis* group," with *Cervus algericus* Lydekker, 1890 from North Africa as the type species and as a subgenus within the genus *Megaceros*. Azzaroli and Mazza (1992, 1993) later elevated the *Megaceroides* taxon to the genus level. Both *Megaceroides algericus* and *Praemegaceros dawkinsi* are difficult species to typify at the genus level, as they represent stunted endemic forms with restricted geographical distribution. Radulescu and Samson (1967) recognized several genera within the "*verticornis* group" and, in addition to *Praemegaceros* Portis, they proposed two new genera: *Allocaenelaphus*, with the type species *Allocaenelaphus arambourgi* (now a junior synonym of *Praemegaceros obscurus* [Azzaroli, 1953]: Croitor and Bonifay, 2001), and *Psekupsoceros*, with the type species *Psekupsoceros orientalis* (now a junior synonym of *Praemegaceros pliotarandoides* [de Alessandri, 1903]: Croitor and Kostopoulos, 2004). According to the Romanian authors, the newly proposed genera represent the early evolutionary stages of mainland large-sized deer.

Hadjouis (1990) conducted a systematic review of *Megaceroides algericus* from the Late Pleistocene and Early Holocene of North Africa, revealing a marked morphological distinction between this African deer and the verticornis-like cervids of Europe and the Mediterranean "dwarfed megacerines." According to Hadjouis (1990), *M. algericus*, which displays strong cranial pachyostosis, exhibits morphological features that are similar to those of Asian *Sinomegaceros*. The distinct and poorly understood adaptations of the African deer, with a very broad skull and particularly small teeth, create an inaccurate impression of the heterogeneity of fossils attributed to *M. algericus* (Croitor, 2004). The craniodental morphology of the endemic *M. algericus* is highly specialized, and therefore this cervid cannot serve as a type species for any genus of fossil European deer (Croitor, 2016). Therefore, *Praemegaceros* is the only acceptable genus name for the arbitrary "*verticornis* group" (Croitor and Bonifay, 2001).

The genus *Praemegaceros* is suggested to be a paraphyletic group that consists of three closely related sister lineages. These include the subgenus *Praemegaceros* Portis, 1920, comprising of the species *P. obscurus* – *P. dawkinsi* (Croitor, 2004; Croitor, 2006a); the subgenus *Orthogonoceros* Kahlke, 1956, consisting of the species *P. pliotarandoides* – *P. verticornis* (Croitor and Kostopoulos, 2004); and a third lineage that includes two sister species, *P. solilhacus* and *P. cazioti*. In this paper, we designate the third lineage as the subgenus *Nesoleipoceros* Radulesco and Samson, 1967. The position of these species among other Pleistocene large-sized European deer has remained uncertain for a considerable period.

Although Azzaroli (1979) placed *P. solilhacus* in the "*verticornis* group," the possible relationship between this deer and other representatives of this group has yet to be fully understood. Azzaroli and Mazza (1993) suggest that *P. solilhacus* is a sister species of the boldrinii-verticornis lineage, which is believed to have developed in parallel from a common ancestor. Abbazzi and Masini (1996) proposed a phylogenetic relationship between *P. solilhacus* and the small-sized *P. dawkinsi* from England, based on the similar reduction of proximal tines in both species. Van der Made (1999) speculated that *P. dawkinsi* is merely a diminutive variant of *P. solilhacus*.

The origin of *P. cazioti* has also remained a mystery for a long time. Depéret (1897) considered this insular deer to be the last survivor of the genus *Eucladoceros*. Radulescu and Samson (1967) suggested that *P. cazioti* is a descendant of a primitive mainland *Praemegaceros*, while Azzaroli (1961, 1979) believed it to be a stunted descendant of a giant mainland *verticornis*-like form with simplified antlers.

The taxonomical problem of "*Dama*-like" deer. The systematic position of small-sized cervines with simple three-pointed antlers remains contentious. De Vos et al. (1995) classified *Metacervocerus pardinensis* and *Metacervocerus rhenanus* as members of the genus *Cervus*, whereas Pfeiffer (1999) placed them in the genus *Dama*. However, the skull shape of *M. rhenanus* is too primitive to be included in either *Dama* or *Cervus*. In contrast to *D. dama*, the pedicles of *Metacervocerus* are longer and sloped backwards, the braincase is relatively long and little flexed, and the bullae tympani are relatively smaller (Croitor, 2006b). Unlike *Cervus elaphus*, *M. rhenanus* is characterized by a relatively longer braincase and a shorter orbitofrontal portion, the relatively longer nasal bones that extend behind the line connecting the anterior edges of orbits, the broad bell-shaped basioccipital, the larger bullae tympani, and the absence of upper canines.

Di Stefano and Petronio (2002) included *M. rhenanus* and *M. pardinensis* in the modern genus *Rusa*; however, this viewpoint is not supported by cranial morphology. Unlike *Metacervocerus*, *Rusa* is characterized by short nasal bones that do not reach the level of the anterior margins of orbits, small bullae tympani, and narrow basioccipital (like *Cervus*), and it possesses upper small canines (like *Cervus*) that should be regarded as a primitive character (Flerov, 1952). Therefore, *Metacervocerus* and *Rusa-Cervus* represent two different evolutionary lineages of Cervinae distinguished by an incompatible mosaic combination of primitive and advanced characters. The analysis of bony labyrinth morphology carried out by Mennecart et al.

(2017) confirmed the hypothesized sister phylogenetic relationship of *M. rhenanus* (= *M. philisi*) with the modern *Axis axis* proposed by Croitor (2014).

The history of the genus *Dama* remains poorly understood due to taxonomic confusions and conflicting opinions regarding the systematics of the small cervids that existed during the European Pliocene and Early Pleistocene, also referred to as the "*Dama*-like deer" (Di Stefano and Petronio, 1998). This informal group includes various Pliocene and Early Pleistocene deer that had a body size comparable to that of modern fallow deer and bore three- or four-pointed antlers. The primary source material for these "*Dama*-like" deer comes from antler remains from the Early Pleistocene at Upper Valdarno, Italy.

Pfeiffer (1999) proposed a phylogenetic reconstruction of small-sized "*Dama*-like" deer from the Early Pleistocene of Europe based mainly on morphological characters of the postcranial skeleton. The primary criteria for character selection were the low variability of the considered characters, including the ontogenetic variability and sexual dimorphism, and the distinct differentiation of the morphological character state (Pfeiffer, 1999). However, postcranial morphology in ruminants is known to be highly influenced by factors such as body mass, locomotion type, character of landscape, and character of the ground surface (Flerov, 1950; Gambarian, 1972; Sutula, 1990; Caloi and Palombo, 1991; Köhler, 1993; Curran, 2012). The cladogram obtained by Pfeiffer (1999: fig. 145) groups *Axis axis*, *Cervus elaphus*, and the stunted fallow deer from the Early Pleistocene of Pirro Nord (Italy) on one side and *C. nestii*, *M. rhenanus*, and most *Dama* species (including *D. dama*, *D. mesopotamica*, and *D. clactoniana*) on the other side. However, Pfeiffer's (1999) results contradict genetic studies (Douzery and Randi, 1997; Randi et al., 1998; Gilbert et al., 2006). Furthermore, *Eucladoceros* is considered quite distant from *C. elaphus*, as per Pfeiffer (1999), but this is contradicted by the recent results obtained by Mennecart et al. (2017).

Di Stefano and Petronio (1998) conducted a similar hierarchical cluster analysis based on morphological features of postcranial bones but obtained different results: *C. nestii* is closely associated with *D. eurygonos* and *A. axis*, while *M. rhenanus* is associated with *D. clactoniana* and *Rusa unicolor*.

Reliable morphological characters are essential for taxonomic and phylogenetic research. However, it is important to be aware of the limitations of some cranial characters, such as the splanchnocranium. For example, the splanchnocranium can be greatly influenced by factors such as dietary adaptations, specific environmental conditions, allometry, insular paedomorphism, and other factors (Flerov, 1952; Solounias and Moelleken, 1993; Janis and Ehrhardt, 1988; Geist, 1998). Therefore, caution should be exercised when using these characters in taxonomic and phylogenetic analyses. The accuracy and completeness of the morphological database are essential for conducting reliable multivariate analyses. In this study, we propose giving special attention to the selection and documentation of the morphological characters used for the diagnoses of cervid taxa (Brooke, 1878; Lydekker, 1898; Flerov, 1952; Azzaroli, 1953; Sokolov, 1959; Heintz, 1970; Korotkevich, 1970; Bouvrain et al., 1989; Bubenik, 1990; Vislobokova, 1990; Azanza and Montoya, 1995; Danilkin, 1999; Azanza, 2000; Webb, 2000; Croitor, 2006b, 2018a, b; Gustafson, 2015).

The taxonomical issues of the genus *Procapreolus*. The genus *Procapreolus* was proposed by Schlosser (1924) to describe small-sized deer with three-pointed antlers similar to those of modern roe deer. While a formal definition of this new genus was not provided, Schlosser included Procapreolus in the arbitrary "*Capreolus* group." *Procapreolus* is distinguished from modern roe deer (*Capreolus capreolus*) by the development of the *Palaeomeryx* fold in lower molars (Schlosser, 1924). Schlosser (1924) explicitly included two species in *Procapreolus*: *Procapreolus latifrons* Schlosser, 1924 from the Late Tertiary of Olan Chorea, Inner Mongolia, and *Cervavus ruetimeyeri* Schlosser, 1903 (spelt as *Cervavus rütmeyeri* in Schlosser, 1924) from the Late Neogene of Mongolia and China. Although Schlosser (1924) noted a striking resemblance of *P. latifrons* with *Cervus cusanus* Croizet and Jobert, 1828 from the Pliocene of Perrier-Etouaries (France), the latter species was not included in *Procapreolus*. Similarly, while Schlosser (1924) mentioned *Cervus* (*Palaeaxis*) *loczyi* Pohlig, 1911 from the Late Miocene of Pannonia, it was included in *Capreolus*. Schlosser (1924: 75) thus suggested that *Procapreolus* from [Inner] Mongolia "was certainly somewhat related to *Capreolus loczyi* Kormos" (*sic*). A more detailed analysis of the relationships among these taxa is needed to clarify their phylogenetic positions.

Korotkevich (1963) was the first to review the genus *Procapreolus*, designating *Procapreolus latifrons* as the type species and including in *Procapreolus* the new species *Procapreolus ucrainica* (*Procapreolus ucrainicus* according to the ICZN Article 31.2 “Agreement in gender”) from the Late Miocene of Ukraine. In the same study, Korotkevich (1963) excluded *Cervavus ruetimeyeri* from *Procapreolus* because the shape of its antlers did not correspond to the genus diagnosis provided by Korotkevich (1963). Subsequently, Korotkevich (1970) included in *Procapreolus* the poorly known species *Cervus* (*Palaeaxis*) *loczyi*, which was not discussed in her previous work, as well as *Cervus cusanus* Croizet and Jobert, 1928, and *Cervocerus wenzensis* Czyżewska, 1960. In light of this nomenclatural act by Korotkevich (1970), *Procapreolus* Schlosser, 1924 becomes a junior synonym of *Palaeaxis* Pohlig, 1911 according to the principle of priority.

However, the sample of fragments of antlers and frontal bones described by Pohlig (1911) is mixed and represents several ontogenetic stages of antler development of a cervid form that is different from *Procapreolus*. The proximal fragment of antler figures on the Table VI is very robust and resembles *Neomegaloceros gracilis* Korotkevich, 1971 from the Late Miocene of Ukraine. The fragment of the frontal bone with a short and robust pedicle (Pohlig, 1911: tab. VI, fig. 3) also matches the morphological condition seen in *Neomegaloceros gracilis*. Therefore, at least a part of the original material of *Palaeaxis loczyi* cannot be included in *Procapreolus*.

Dong and Ye (1997) have questioned the validity of *Procapreolus latifrons*, suggesting that it is a variation of "*Cervavitus novorossiae*" from the Late Neogene of China. However, according to the generally accepted opinion, the Late Neogene cervid remains from China attributed to *Cervavitus novorossiae* are poorly understood and distinct from the original Late Miocene findings of this species from southeastern Europe (Azzaroli, 1953, 1992; Czyżewska 1968; Di Stefano and Petronio, 2002). The unresolved taxonomic issues have led to cautious use of the genus name Procapreolus, which potentially could be polyphyletic (Croitor and Stefaniak, 2009; Croitor, 2014). Thus, a detailed taxonomic study is required to resolve the validity of *Procapreolus*.

The original description of *Procapreolus latifrons* by Schlosser (1924) is detailed and provides a comprehensive description of this species. The diagnosis is based on a series of fragmented antlers, each showing a uniform specific morphology (Schlosser, 1924). The type specimen (Schlosser, 1924: p. 76, fig. 4 C) is characterized by a thin beam with a diameter of 25 mm and a comparatively high position of the first ramification, approximately 95 mm above the burr. The proximal part of the antler lacks pearling and tubercles, an important morphological characteristic that distinguishes antlers of *Procapreolus* from those of modern *Capreolus*. The frontal bones are broad, with a breadth of 45 mm in the type specimen, and flat. The pedicles are gently compressed anteroposteriorly and are quite long. The cross-section of the antler beam is nearly circular, and antler beams are strongly curved outwards and backwards (Schlosser, 1924). The length of an antler tine may reach 115 mm. The fact that *P. latifrons* was based on a series of antler remains rules out the possibility that the type specimen is just an individual random variation of the antler. The basal fragments of antler from the *Hipparion* fauna of China reported by Schlosser (1903: tab. XI, fig. 30) as *Cervus* sp. most probably also belong to *P. latifrons*. Another finding from the Hipparion fauna of China is worth mentioning here, namely the antlered braincase and antler fragments of a small-sized cervid figured by Zdansky (1925: Pl. VI; Pl. V, fig. 5) that show a great morphological affinity with *Procapreolus*. Additionally, *Metacervulus mongoliensis* Vislobokova, 1983, a small-sized cervid form from the Pliocene deposits of the Great Lakes

Depression, Mongolia (Vislobokova, 1983), is interesting in this context. This cervid shows a close morphological affinity with the type specimen of *P. latifrons* and is indeed very close to *P. latifrons*, if not synonymous with it. Therefore, remains of small-sized deer with a morphology that is specific for *Procapreolus* (long thin beam with circular cross-section and a very high position of the first ramification) are relatively common in the Late Tertiary of China and Mongolia.

The dental remains found in association with *P. latifrons* antlers correspond to the diagnosis of the genus *Procapreolus* as proposed by Korotkevich (1963, 1970). The upper canines are large, reaching at least 50 mm in length. The fourth lower premolar (P_4) is characterized by an advanced molarization, and the lower molars are enforced with ectostylids and an anterior "fold of compression" (Schlosser, 1924). The absence of the *Palaeomeryx* fold in the lower molars of *P. latifrons* does not preclude the inclusion of the European forms in *Procapreolus* since the *Palaeomeryx* fold follows a trend toward reduction in *P. moldavicus* (Croitor and Stefaniak, 2009) and is completely lost in *P. cusanus* (Heintz, 1970). Therefore, *Procapreolus* Schlosser, 1924 should be considered a valid genus based on the species *P. latifrons*.

At least seven species of *Procapreolus* have been identified from the Late Miocene and Pliocene of Europe. Despite their similar antler morphology, they can be differentiated based on their dental characteristics, such as the presence of a cingulum in upper molars and a *Palaeomeryx* fold in lower molars (Croitor, 2018b). In Western Europe, *Procapreolus pyrenaicus* (Depéret, 1890) has been found in the Early Pliocene of Roussillon (France) and *P. cusanus* (Croizet and Jobert, 1828) in the Early Villafranchian of France and Italy (Heintz, 1970; Abbazzi et al., 1995; Dong, 1996). *P. cusanus* is unique among the species in the genus due to its flattened antlers, which may have up to five tines in rare cases (Heintz, 1970). In Eastern Europe, remains of *Procapreolus* have been found, including *P. ucrainicus* Korotkevich, 1963 (= *P. ukrainicus* Korotkevich, 1965, an unjustified emendation of the species name) from the Late Miocene of Ukraine, *P. florovi* Korotkevich, 1974 from the final stage of the Miocene of Ukraine (Korotkevich, 1974b), *P. pentelici* (Dames, 1883) (= *Pliocervus graecus* Azanza, 1995) from the Turolian-Ruscinian boundary of Pikermi and Maramena, Greece (Azanza, 1995), *P. vesti* (Korotkevich, 1970) (= *Pliocervus kutchurganicus vesti* Korotkevich, 1970) from the mixed Pliocene fauna of the Kosiakinsky Quarry (Ciscaucasia, Russia), and *P. moldavicus* (Janovskaya, 1954) from the Pliocene of Eastern Europe (Croitor and Stefaniak, 2009).

The systematical position and phylogenetic relationships of *Arvernoceros*. The genus *Arvernoceros* was first proposed by Heintz (1970) to include *Cervus* ardei Croizet and Jobert, 1828 from the Late Pliocene of France. *Arvernoceros ardei* is characterized by its highly distinctive antler morphology, which features a flattened first tine with an accessory prong and a small distal palmation terminated with three tines. Heintz (1970) suggested that *A. ardei* is a forerunner of *M. giganteus* due to the flattened basal tine and the strong development of the lingual cingulum in upper molars, which are traits that are also associated with the latter species.

Arvernoceros verestchagini David, 1992, which has been found in the Early Pleistocene of Moldova, exhibits a similar antler morphology as *A. ardei*, but is notably larger and does not feature distal antler palmation. Van der Made and Tong (2008) have noted that the overall pattern of antler construction in *Arvernoceros* is reminiscent of that seen in *Sinomegaceros*. According to Croitor (2009, 2018a), the antler shape of *Arvernoceros* is highly similar to that of *Rucervus*, a modern deer genus. Genetic evidence indicates that *Rucervus duvaucelii* diverged very early from the main group of Old World deer (together with *Axis axis*) during the Late Miocene (Pitra et al., 2004).

Systematical position of *Eucladoceros*. The phylogenetic relationships of *Eucladoceros* have long remained unclear. In general, the origin and phylogenetic relationships of the genus *Eucladoceros*, which is characterized by a unique comb-like antler shape, have received relatively little attention from researchers. Flerov (1952) initially proposed that *Eucladoceros* could be a forerunner of large-sized Quaternary cervid genera such as *Megaloceros*, *Cervalces*, and *Alces*, but this viewpoint was not supported by subsequent research. Although the antler morphology of *E. ctenoides* bears some resemblance to that of the modern *Przewalskium albirostris*, caution is needed when inferring evolutionary relationships based solely on antler shape. In this regard, I previously argued that the similarity between *Eucladoceros* and *Przewalskium* may be superficial and that the inclusion of *Eucladoceros* within the *Przewalskium-Rusa-Cervus* lineage is unlikely (Croitor, 2014). However, recent studies examining the morphology of the body labyrinth have revealed a close affinity between *E. ctenoides* and *Cervus elaphus* (Mennecart et al., 2017). Consequently, it is highly probable that there exists a close evolutionary relationship between *Eucladoceros* and *Przewalskium*.

The poorly known continental fossil deer. Only one specimen of the poorly known *Neomegaloceros gracilis* Korotkevich, 1971 has been found so far from the Late Miocene of the Odesa Region, Ukraine. Korotkevich described this species as a forerunner of *Praemegaceros verticornis*, as its antler exhibits distal palmation and an additional tine, which was interpreted as a homolog to the posterior tine in *Praemegaceros*. However, the general antler shape of *Neomegaloceros* shows no similarity to *Praemegaceros*, and the distal palmation is only present in advanced forms of *Praemegaceros*. The functional significance of the so-called "posterior tine" needs to be understood, as it appears in several cervid lineages such as *Rangifer*, *Megaloceros*, *Praedama*, and some *Sinomegaceros*.

Pseudalces mirandus Flerov, 1962 is another poorly understood ruminant from the Pliocene of the Kosiakinsky Quarry in the southern part of European Russia, and is believed to be one of the earliest giant cervid forms possibly related to the evolutionary radiation of Alcinae/Alcini. The type specimen of *P. mirandus* is a fragment of a skull with a right upper tooth row and frontal bone, with unknown antlers.

Tamanalces caucasicus Verestchagin, 1957 from the Early Pleistocene of the Tamani Peninsula (south of European Russia) is based on a small fragment of the frontal bone with pedicle and basal portion of antler. According to Vislobokova (1990), *Tamanalces* is an extinct branch of true elks (Alcinae), but this assumption requires confirmation.

The systematic position of endemic insular deer. The endemic dwarfed deer from the Pleistocene of the Mediterranean exhibit extreme dwarfism, as well as evolutionary simplification and specialization of their antlers. This strong evolutionary specialization of antlers and cranial morphology complicates the understanding of the origin of insular deer and their relationship with continental forms. The phenomenon of insular dwarfism is summarized by Foster's Rule (Foster, 1964), which posits that on islands, large mammals evolve to smaller body sizes, whereas mammals of small body sizes on islands typically enlarge. Insular dwarfism arises due to several factors, including missing predator selective pressure in unbalanced island faunas lacking terrestrial predators, the advantage of the high-density population of a small-bodied form over the low-density population of a large-bodied form in the insular conditions, and the available ecological niches in insular ecosystems that require a smaller body size (Foster, 1964; Sondaar, 1977; Caloi and Palombo, 1994).

Sondaar (1977) and van der Geer (2005) regarded insular dwarfism as a paedomorphic phenomenon that is expressed in the relative increase of braincase, simplification of horns and antlers (with consecutive change in their function), disproportional diminishing of the body, and limb shortening. Due to the lack of pressure from terrestrial mammal predators, insular herbivores acquire anterior orientation of orbits that achieves stereoscopic vision, reduce their olfactory abilities, and completely lose the ability to run fast due to the increased limb stability and simplification of the limb structure (van der Geer, 2005). Multiple studies of dwarfed island deer, mainly from Mediterranean islands, have revealed a general evolutionary trend towards antler diminishing and simplification, muzzle shortening, reduction of preorbital fossae and ethmoidal openings, and decreased fast locomotion abilities (Azzaroli, 1961, 1979; Sondaar, 1977; Palombo, 1986; Caloi and Palombo, 1994; Croitor, 2001).

Geist (1998) described another curious zoogeographic instance from modern South American fauna. As the Neotropic fauna lacks effective pursuing predators, "South American deer consequently evolved as small-bodied saltatorial runners with little endurance" (Geist, 1998: p. 110). The antlers of South American deer, as in insular dwarfed forms, are rather small, simplified, vestigial or even vanished. These examples suggest that the isolation of islands is not the decisive condition in the evolution of "island dwarfs".

The predominance of cervids among the insular Mediterranean herbivores is an interesting fact that deserves special attention. The successful colonization of Mediterranean islands by bovids is restricted to rather exceptional cases of Nesogoral from the Plio-Pleistocene of Sardinia, and *Myotragus* from the Balearic Islands, which probably colonized the islands during the Messinian crisis and became extinct just 6000-4000 years ago. According to obtained molecular data, *Myotragus* has a basal position to the *Ovis* group (Lalueza-Fox et al., 2000). There are no instances of successful island colonization by Perissodactyla. Instead, cervids repeatedly colonized many Mediterranean islands and gave origin to many endemic insular forms.

According to Azzaroli (1961, 1971, 1979), the majority of deer species found on Mediterranean islands belong to the "*verticornis* group" of the *Megaceros* Owen genus, while a few island forms represent the modern genus *Cervus*. This viewpoint has been accepted by many authors (Radulesco and Samson, 1967; Caloi and Malatesta, 1974; Caloi and Palombo, 1994; Gliozzi and Malatesta, 1982; Palombo, 1986). Radulescu and Samson (1967) proposed to include all island "megacerines" in a single genus *Nesoleipoceros* with the type species *Cervus cazioti* Depéret, but this taxonomical solution is questionable as it suggests uniting several lineages that colonized islands independently and evolved parallel (or even convergent) adaptations to insular conditions. Kuss (1975) grouped deer species from eastern Mediterranean islands in the genus Candiacervus, but their relationship with continental forms remains unclear. Gliozzi and Malatesta (1982) accepted the generic name *Praemegaceros* for insular "megacerines" and included *Nesoleipoceros* in the synonymy of *Praemegaceros*. According to the cited authors, the type species of *Nesoleipoceros* differs from its mainland relatives only in size and some morphological features correlated with size reduction. However, Gliozzi and Malatesta (1982) distinguished another distinct lineage of dwarfed "megacerines" from the middle Pleistocene of South Italy and the middle and late Pleistocene of Sicily (*Praemegaceros calabriae* and *P. carburangelensis*) and placed them in the new subgenus *Notomegaceros*. The short face and rounded, convex braincase of the deer from Calabria and Sicily were regarded by Gliozzi and Malatesta (1982) as paedomorphic characteristics accompanied by body size reduction. According to the recent systematic revision carried out by Abbazzi et al. (2001), those cervids belong to the genus *Dama*.

Thus, the taxonomic classification of insular deer species in the Mediterranean is a complex and ongoing subject of study. While some authors have proposed various taxonomic solutions, there is still much debate and uncertainty surrounding the systematic position of these species.

Continental endemic deer from the Pleistocene of Europe. The Pleistocene deer endemic to Europe represents a significant paleobiogeographic feature of the western Palearctic. As insular dwarfs, the continental endemics exhibit specialized and often simplified shapes of antlers. The restricted geographic distribution of these cervids has a rather refugial character, and their systematic position and phylogenetic relationships remain unresolved in most cases.

In the middle Pleistocene site of Lunel-Viel in the South of France, several antlers of a medium-sized deer with unusual morphology were described as a new species Euctenoceros mediterraneus by Bonifay in 1967. This deer was believed to be a Villafranchian survivor that lived during the interglacial fauna of Southwestern Europe. Later, Rouzaud et al. in 1990 ascribed two fragmented antlers from the late Middle Pleistocene deposits of L'Igue des Rameaux to *Euctenoceros mediterraneus*, stressing the uncertain generic position of this species. The scarce characters of the material used for the original description of the species "*Euctenoceros*" *mediterraneus* did not provide sufficient morphological data to reveal its systematic position, while the traits of antlers and pedicles available for observation clearly showed a strong evolutionary specialization. The deer from Lunel-Viel is placed in the endemic genus *Haploidoceros* according to Croitor et al. (2008).

Other endemic continental cervid forms include *Praemegaceros dawkinsi* from the Middle Pleistocene of the Cromer Forest bed Formation in England, *Praedama matritensis* from the Late Pleistocene of the Iberian Peninsula, and *Rucervus radulescui* from the Early Pleistocene of Valea Graunceanului in Romania. The origin of these continental endemics is related to forerunners from older faunas that survived in climate refugia.

The study of endemic fossil deer from the Western Palearctic presents a very interesting and complex field that is still imperfectly understood. These insular dwarfs display specialized and often simplified shapes of antlers, and their restricted geographic distribution has a rather refugial character. The systematic position and phylogenetic relationship of many Pleistocene endemic deer species from Europe remain unresolved, and further research is needed to clarify their taxonomic status. The discovery of new species and the revision of old ones using modern techniques such as hierarchical clustering can help to provide a better understanding of the paleobiogeography of fossil deer and their evolutionary history.

1.3. Conclusions to the Chapter 1

An overview of the history of systematic and taxonomic studies of fossil deer reveals several issues that are yet to be resolved:

1. While the current classification of the Cervidae family into two subfamilies - Cervinae and Capreolinae - was proposed in the late 19th century, many questions regarding the origins of some modern groups (such as the telemetacarpal deer) and the systematic position of many fossil species and taxa remain unclear or speculative (Croitor, 2021).

2. The systematic position of some fossil deer from the Late Miocene of Europe remains unresolved, such as in the case of the genus *Pliocervus*, or speculative, such as with holometacarpal deer included in the genus *Cervavitus* (Croitor, 2021a).

3. The taxonomical status and systematic position of the tribe Megalocerotini (= Megacerini), also known as "giant deer," remains contradictory and requires resolution. The unclear understanding of this group obscures the main features of the evolution of continental Pleistocene Cervinae (Croitor, 2006a, 2016; 2021b).

4. The unresolved taxonomical and systematic issues of small-sized Cervinae from the Pliocene and Early Pleistocene of Europe, known as "*Dama*-like deer", do not provide a complete understanding of the early evolutionary stages of modern Palearctic genera (Croitor, 2006b; Croitor and Robinson, 2020).

5. Poor knowledge of the origin of most of the Pliocene and Pleistocene genera of the Western Palearctic (such as *Arvernoceros*, *Eucladoceros*, *Praemegaceros*, and *Praedama*) hinders the understanding of biogeographic evolution at the continental scale, the understanding of modern deer biodiversity origin, and the influence of climate change on the cervid biodiversity in the past and the present (Croitor, 2018a, b, 2021b).

2. METHODOLOGICAL APPROACH TO THE STUDY OF CERVID SYSTEMATICS AND PHYLOGENY

2.1. Revision of type specimens

The present investigation encompasses a set of 50 type specimens obtained from old historical collections alongside supplementary samples originating from the type localities. An exhaustive review of the type material, comprising holotypes, syntypes, lectotypes, and neotypes, is complemented by a thorough examination of original species publication sources as well as consequential nomenclatural acts such as revisions, taxonomical status changes, alterations of genus and name combinations, and synonymy.

2.2. Methodological issues and applied research methods

The primary methodological challenge in the present study is the disparity in the taxonomical and systematic approaches to the description of cervid species used by palaeontologists and neontologists. The diagnosis of modern cervid species, and particularly genera, relies heavily on cranial morphology (Pocock, 1942, 1943a, b, c; Flerov, 1952; Sokolov, 1959; Danilkin, 1999; Meijaard and Grooves, 2004). In contrast, definitions of the majority of fossil deer taxa are primarily based on antler morphology (Azzaroli, 1953; Heintz, 1970; Korotkevich, 1970; Pfeiffer, 1999; Di Stefano and Petronio, 2002). This methodological discrepancy is due to the morphological uniformity of cervid craniological material and the relative rarity of well-preserved skulls in the fossil record, making it difficult, if not impossible, to compare modern and fossil cervid species and forms. Therefore, this study pays special attention to the detailed description of cranial findings, particularly rare complete specimens. Where possible, the proposed updated diagnoses are supplemented with craniodental characteristics to align the taxonomy of fossil deer with the taxonomical standards in neontology.

The applied measurements follow the methodology proposed by von den Driesch (1976). The angle between the neurocranium and splanchnocranium is measured according to Vislobokova (1990). This paper uses generally accepted and well-known terminology (Heintz, 1970; Lister, 1987; Vislobokova, 1990), while avoiding the specific and lesser-known terminology for dental and antler morphology proposed in recent publications. The estimation of body mass used for eco-morphological descriptions of fossil cervid forms is based on craniodental measurements according to the regression equations proposed by Janis (1990). The Cervid systematics proposed by Groves (2005) and Groves and Grubb (2011) is applied in the present study.

To estimate the functional length of the tooth row, the measurements of tooth rows are taken as the maximal possible value, which is crucial for the evolutionary and morpho-functional approach. The measurements of isolated teeth are taken as the maximal mesiodistal crown length (L) and lingual-labial breadth of the crown (D). The former often corresponds to the length of the grinding surface of a tooth, while the latter represents the maximal basal breadth for upper cheek teeth and the maximal breadth for lower cheek teeth.

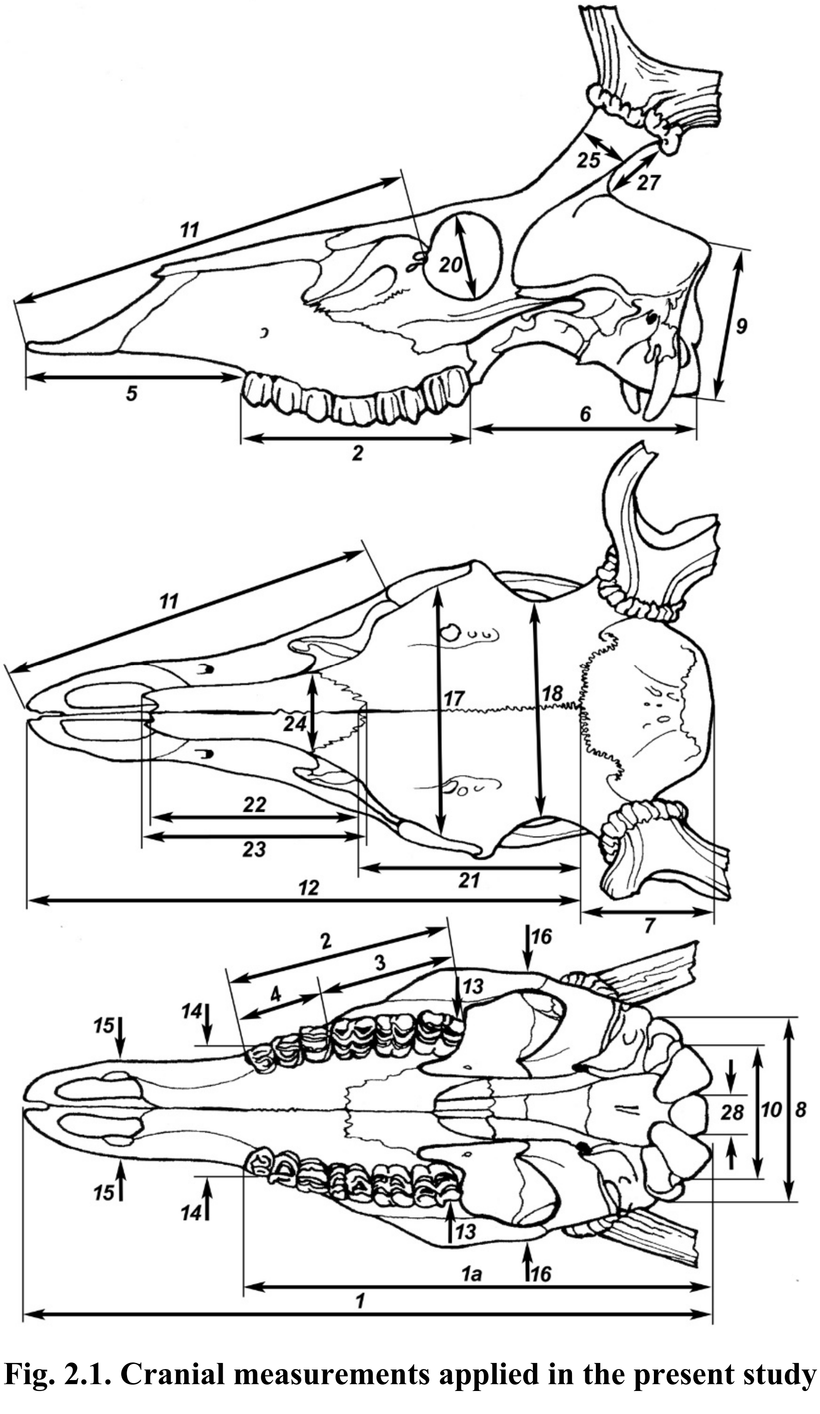

Fig. 2.1. Cranial measurements applied in the present study

The cranial measurements used in the present work (Fig. 2.1):

1. The condylobasal length of the skull (CBL): the measurement is taken from the prosthion point to the posterior edges of the occipital condyles.

1a. The condylodental length of the skull (CBD): the measurement is taken from the anterior edge of the P^2 alveolus to the posterior edges of the occipital condyles.

2. The length of the upper tooth row (L P^2-M^3): the measurement is taken from the anterior edge of the P^2 crown to the posterior edge of the M^3 crown.

3. The length of the upper molar series (L M^1-M^3): the measurement is taken as the maximal value (from the anterior edge of the M^1 crown to the posterior edge of the M^3 crown).

4. The length of the upper premolar series (L P^2-P^4): the measurement is taken as the maximal value (from the anterior edge of the P^2 crown to the posterior edge of the P^4 crown).

5. The length of the anterior part of the skull before the tooth row (L P^2-Pr): the distance between the anterior edge of the alveolus of P^2 and the prosthion point.

6. The length of the posterior part of the skull (LPs): the distance between the anterior edge of the alveolus of M^3 and the posterior edge of the occipital condyles.

7. The length of the braincase (LBr): the distance between the bregma point and the opisthocranion.

8. The occipital breadth (DOcp).

9. The occipital height (HO): measured from the basicranium to the opisthocranion.

10. The breadth of occipital condyles (DOC).

11. The length of face (LF): measured from the anterior edge of orbits to prosthion.

12. The length of the anterior part of the skull (LAnt): measured from bregma to the prosthion.

13. The skull breadth at M^3 (DMM): the measurement is taken between the alveolar edges in the middle of the right and left M^3.

14. The skull breadth at P^2 (DPP): the measurement is taken between the alveolar edges in the middle of the right and left P^2.

15. The breadth of the muzzle (DMz): the measurement is taken behind the upper canines or the suture between maxillary and premaxillary bones.

16. The maximal breadth at zygomatic arches (DZg).

17. The breadth above orbits (DO): the measurement is taken above the orbital centres.

18. The frontal breadth (DFr; in males only): the measurement is taken at the frontal constriction before the pedicles.

19. The breadth of the neurocranium (DNr): the measurement is taken behind the pedicles in males and as a maximal breadth of the braincase in females.

20. The diameter of the orbit (DOrb; vertical).

21. The length of the frontal suture (LFr): from bregma to nasion.

22. The length of the nasal suture (LNas): from nasion to rhinion.

23. The maximal length of the nasal bones (LNmax).

24. The breadth of the nasal bones (DNas)

25. The anteroposterior diameter of the pedicle (DAPpd): measured at the upper part of the pedicle.

26. The lateromedial diameter of the pedicle (DLMpd): taken as the previous measurement.

27. The height of the pedicle (Hpd): the lesser measurement is taken at the posterolateral side of the pedicle.

28. The breadth of the foramen magnum (DFM).

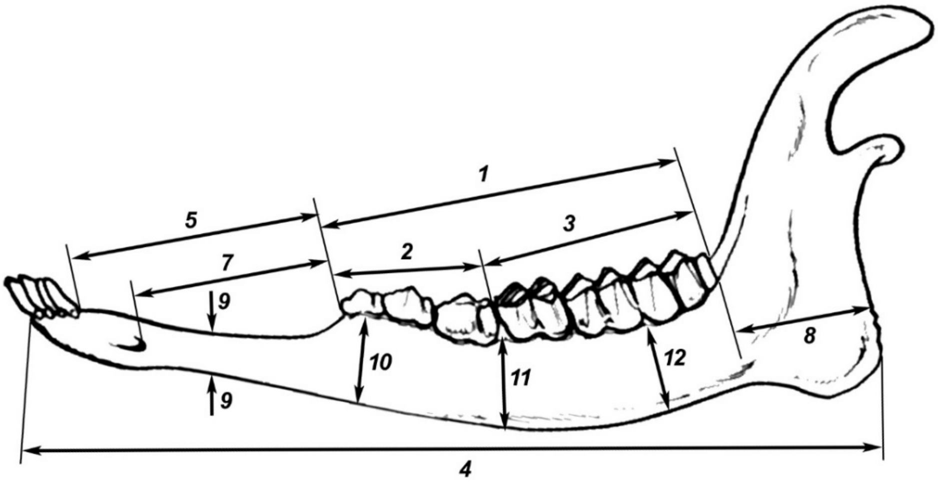

Fig. 2.2. Mandible measurements applied in the present study

The measurements of the lower mandible used in the present work (Fig. 2.2):

1. The length of the lower tooth row (L P_2-M_3): the measurement is taken from the anterior edge of the P_2 crown to the posterior edge of the M_3 crown.

2. The length of the lower premolar series (L P_2-P_4): the measurement is taken as the maximal value (from the anterior edge of the P_2 crown to the posterior edge of the P_4 crown).

3. The length of lower molar series (L M_1-M_3): the measurement is taken as the maximal value (from the anterior edge of the M_1 crown to the posterior edge of the M_3 crown).

4. The length of the horizontal mandibular ramus (LHR): measured from infradentale (alveolar edge between the first incisive) to the posterior edge of the processus angulatus (angulus mandibulae).

5. The length of the diastema (L P_2-C): measured from the anterior edge of the alveolus of P_2 to the posterior edge of the alveolus of the lower canine (C).

6. The distance between P_2 and the mandibular symphysis (L P_2-Sym): measured from the anterior edge of the alveolus of P_2 to the symphysis of the mandible.

7. The distance between P_2 and the foramen mentale (L P_2-FM): measured from the anterior edge of the alveolus of P_2 to the foramen mentale.

8. The distance between M_3 and the posterior edge of the mandible (L M_3-Post): measured from the posterior edge of M_3 to the posterior edge of the processus angulatus.

9. The height of the diastema (HD): the height of the lowest part of the mandible between P_2 and C.

10. The height of the mandible below P_2 (H\P_2): the height of the horizontal ramus of the mandible is taken as the distance from the anterior edge of the alveolus of P_2 to the point on the lower edge of the mandible below P_2 (the taken measurement is perpendicular to the lower edge of the mandible).

11. The height of the mandible below M_1 (H\M_1): the height of the horizontal ramus of the mandible is taken as the distance from the alveolus of M_1 in the middle to the point on the lower edge of the mandible (from the lingual side).

12. The height of the mandible below M_2-M_3 (H\M_2-M_3): the height of the horizontal ramus of the mandible is taken as the distance from the alveolar edge between M_2 and M_3 to the point on the lower edge of the mandible (from the lingual side).

13. The mandibular thickness below P_2 (D\P_2).

14. The mandibular thickness below M_1 (D\M_1).

15. The mandibular thickness below M_2-M_3 (D\M_2-M_3).

The measurements used in this study are consistent with the craniodental variables used by Janis (1990) for body mass predictions. The estimated body mass of the fossil deer was calculated as a rounded sum of the obtained body mass predictions based on different cranial and dental measurements.

For small-sized deer, antler morphology is described using the terminology applied by Heintz (1970) and Lister (1987). The first or basal tine is situated on the anterior side of the beam close to the burr. In the case of the red deer (*Cervus elaphus*), the first brow and the second bez tines are recognized. The next tine situated on the anterior side of the middle part of the beam is called the middle tine (the trez tine in *Cervus*). The tine situated on the posterior side of the beam is called the posterior tine, and the distalmost antler branches are called crown tines. The height of the first antler ramification is usually taken from the lateral side, except when the antler beam is curved, in which case the height of ramification is taken from the convex side of the beam. Similarly, the length of segments (parts of the antler beam between two ramifications) is measured from the convex side of the beam. The total antler length is measured along the antler beam from the burr to the distalmost antler tine.

Several nomenclatural schemes designating antler tines and other morphological elements in antlers of large-sized deer (genera *Praemegaceros*, *Eucladoceros*, *Megaloceros*) have been proposed in the literature (Kahlke, 1956; Radulesco and Samson, 1967; Azzaroli and Mazza, 1992, 1993; Croitor, 2006a). The idea of homology of antler tines in different genera (Kahlke, 1956; Azzaroli and Mazza, 1992) is helpful in reconstructing phylogenetic relationships among extinct cervid genera. The terminology used in this study is largely based on previous terminological systems with some modifications (Croitor, 2006a). The antler tine situated just above the burr is called the subbasal tine (= tine A: Kahlke, 1956; = tine 1; Radulesco and Samson, 1967; = spurious tine: Azzaroli and Mazza, 1992). The second proximal tine situated on the medial side (or dorsal, if the antler is oriented in the natural position on the skull) of the beam is called the dorsal tine (= tine E: Kahlke, 1956; = tine 2: Radulesco and Samson, 1967; = outer tine in *Praemegaceros*, = inner tine in *Eucladoceros*: Azzaroli and Mazza, 1992). The third proximal tine situated on the anterior side of the beam is called the basal tine (= outer tine in Eucladoceros: Azzaroli and Mazza, 1993). The fourth tine situated on the anterior side of the beam is called the middle tine (= tine M: Kahlke, 1956; = tine 3: Radulesco and Samson, 1967; = anterior tine: Azzaroli and Mazza, 1993). The antler tine inserted on the posterior side of the beam is referred to as the posterior tine (= tine 4: Radulesco and Samson, 1967), while the tines situated above it are called the crown tines. In the present study, the nomenclatural scheme for each type of antler is maintained for two reasons. Firstly, the homology of antler tines in different cervid lineages is not yet proven, so unifying the nomenclatures may give a false impression of their homological nature. Secondly, preserving the nomenclatural schemes already used in the literature helps to avoid terminological confusion.

2.3. Morphological criteria of a genus

When selecting morphological criteria for a genus, it is important to consider the ecological and functional significance of a morphological feature, as well as its evolutionary history. In ruminants, limb bone morphology is influenced by environmental and biomechanical factors, and is of minor interest in systematic studies at the genus and subgenus level (Vislobokova, 1990). Postcranial morphology, on the other hand, is heavily influenced by factors such as the species' ecology, locomotion strategy, landscape character, and body weight (Flerov, 1952; Köhler, 1993; Croitor, 2006b; 2014).

In the systematics of modern and fossil deer, cranial morphology (excluding exosomatic parts such as premaxillary bones, preorbital fossae, and relative size of tooth row) provides a set of plesiomorphic characters that have taxonomic value at the genus level (Pocock, 1942, 1943a, b, c; Flerov, 1954; Sokolov, 1959; Janis and Scott, 1987; Vislobokova, 1990). These characters include: 1) proportions of the facial and cerebral parts of the skull; 2) shape of the parietal bones; 3) shape and relative length of the frontal bones; 4) position, orientation, and length of pedicels; 5) size, position, and shape of the orbits; 6) morphology and size of the ethmoidal openings; 7) position and length of the nasal bones; 8) position and shape of the frontonasal suture; 9) position of the upper dentition row relative to the orbits; 10) shape of the basioccipitale; and 11) morphology and proportions of the lower mandible (including the shape of the processus angularis and the angle between the horizontal and ascending portions).

Dentition morphology is also commonly used as a morphological criterion at the genus level. The following characteristics have been suggested by various authors (Schlosser, 1924; Pocock, 1942, 1943a, b, c; Flerov, 1952, 1962; Heintz, 1970; Azzaroli, 1985; Janis and Scott, 1987; Vislobokova, 1990): 1) angle between labial and lingual slopes of upper molars, which is correlated to tooth crown height; 2) presence or absence of upper canines; and 3) development of Palaeomeryx fold or presence of its traces. The molarization of the lower fourth premolar (P_4) and the length ratio between the lower premolar and molar series are also often used as morphological criteria for the genus in cervid systematics (Vislobokova, 1990).

Janis and Lister (1985) noted a high level of individual variation in the fourth premolar (P_4) among pecorans and recommended caution when using this character for taxonomy studies. For example, the molarization of P_4 in *Cervus elaphus* varies from 8% to 47% across different populations. Although P_4 appears to be quite variable in the subfamily Cervinae, the high molarization of P_4 remains relatively constant in some genera (*Dama*, *Megaloceros*) and may be regarded as a genus-specific character in some cases. In contrast, the molarization of P_4 is less variable in the subfamily Capreolinae.

The premolar/molar ratio is widely used to characterize evolutionary specialization within the subfamily Cervinae, where a relatively short series of premolars is considered an advanced feature in the plesiometacarpal deer (Vislobokova, 1990). This evolutionary trend is often accompanied by an increase in the grinding function of the cheek tooth row and a reduction in the cutting function of the lower premolars. However, this pattern is specific to the subfamily Cervinae; in Capreolinae, the premolar/molar ratio is relatively constant while the molarization of lower premolars is highly advanced (Croitor, 2014). For example, P_4 in *Alces* and *Rangifer* evolves into a functional analogue of a molar, while P_3 also evolves a degree of molarization, which further enhances the grinding function of the lower cheek tooth row.

Therefore, the taxonomic significance of craniodental characters such as the molarization of P_4, molar/premolar ratio, and other cranial and dental features should be evaluated in the context of other correlated characters and the broader systematic context of each cervid species.

The taxonomic significance of antler morphology is limited to the general pattern of antler construction that is shared by the species within a given genus.

2.4. Morphological criteria of a species

Species descriptions are typically based on exosomatic characters that are influenced by intraspecific social interactions and environmental factors (Azzaroli, 1953, 1992; Flerov, 1952; Vislobokova, 1990; Geist, 1998). In the case of cervids, important cranial and dental characters include: 1) the relative length of the muzzle (premaxillary length and length of diastema); 2) the shape of premaxillary bones; 3) the length of nasopremaxillary suture; 4) the size and degree of development of preorbital fossae; 5) the size and shape of bullae tympani; 6) the shape and relative length of frontal appendages (pedicles); 7) the development of the cingulum, the *Palaeomeryx* fold and other additional enamel folds; 8) the ratio between premolar and molar tooth series length; and 9) the molarization of lower fourth premolar (P_4). These morphological features generally reflect the ecological niche of a species (Pocock, 1942, 1943a, b, c; Janis and Scott, 1987).

Although cervid antlers are highly variable, they represent an essential organ of communication that ensures genetic isolation between species. Details of antler morphology reflect characteristic intraspecific signals of communication and a specific rutting behavior, serving as a good genetic barrier between true species. As such, antler morphology is an important taxonomic criterion for cervid species, with characters such as: 1) the direction, shape, and length of the antler beam; 2) the number of tines; 3) the development of palmation; 4) the reduction of antler tines and the general simplification of antlers; and 5) the development of specific tines (such as the middle and posterior tines). Proportions of limb bones and body size are used in species definition only in combination with these other characters (Flerov, 1952).

2.5. Cluster analysis of diagnostic characters

In this study, we utilized a multivariate cluster analysis of cranial, dental, and antler characters to assess their taxonomic value and provide support for the systematic position of extinct deer species. To achieve this, we computed the hierarchical clustering paired group algorithm UPGMA using the Jaccard Similarity Index for presence-absence data (PAST-3 application: Hammer et al., 2001). Additionally, the cophenetic correlation coefficient was calculated to determine how accurately the dendrogram reflects the original, unmodeled data points (Farris, 1969).

Due to incomplete data on cranial morphology, we incorporated several assumptions in our dataset, primarily by ascribing a primitive condition for missing morphological characters.

To distinguish between advanced and primitive conditions for morphological characters, we employed the classification system proposed by Vislobokova (1990) in our cluster analysis:

1) Shape of basioccipital: 0, wedge-shaped; 1, bell-shaped (broadened at the pharyngeal tuberosities);

2) Upper canines: 0, absent (advanced condition); 1, present (primitive condition);

3) Pedicles: 0, long (pedicle height exceeds the pedicle diameter; primitive condition); 1, short (pedicle height is smaller than, or equal to, the pedicle diameter; advanced condition);

4) Pedicles: 0, sloped backwards (primitive condition); 1, set vertically (advanced condition);

5) Terminal crown type: 0, absent, 1, present; this crown type is characteristic of modern red deer (*Cervus elaphus*) that in its simplest variant represents a simple fork composed of two equally-sized crown tines oriented in the rostral plane perpendicular to the axis body;

6) Posterior crown type: 0, absent, 1, present; this crown type is characteristic of modern fallow deer (*Dama dama*) that in its simplest variant represents several tines inserted on the posterior side of the beam;

7) Length of nasal bones: 0, short (the posterior edge of nasals does not reach the level of the anterior edges of the orbits; primitive condition); 1, long (the nasal bones extend behind the level of the anterior edges of the orbits; advanced condition);

8) Cingulum on upper molars: 0, absent; 1, present (specialized dental morphology);

9) Protoconal fold on upper molars: 0, absent; 1, present (specialized dental morphology);

10) Position of the first antler ramification: 0, low (more or less equal to the antler base diameter); 1, high (significantly exceeds the antler base diameter);

11) Height of the cheek teeth crowns: 0, brachydont (primitive condition); 1, mesodont (advanced condition);

12) Length of the orbitofrontal part of the skull: 0, short (the anterior edge of the orbit is situated above M^3 or M^2; primitive condition); 1, long (the anterior edge of the orbit is situated behind M^3; the advanced condition in the *Cervus* lineage);

13) Braincase shape: 0, unflexed (primitive condition); 1, flexed (advanced condition).

14) Antler bauplan type: 0, “inadaptative” (the anterior tine of the second bifurcation is longer than the posterior tine); 1, “adaptative” (the anterior tine of the second bifurcation is shorter than the posterior tine).

2.6. Geochronology of Late Neogene and Quaternary

The present study is based on the updated geochronological timescale ratified by the International Union of Geological Sciences in 2009. According to this timescale, the lower boundary of the Quaternary period and the Pleistocene epoch boundary are lowered until the base of the Gelasian Age at 2.58 million years ago (Gibbard and Head, 2009; Gibbard et al., 2010). The Miocene/Pliocene boundary is established at 5.3 million years ago (Steininger et al., 1989).

The geological timescale is subdivided into Mammal Neogene Faunal Zones (MN), a broadly accepted biostratigraphic scale based on the European mammal paleontological record (Mein, 1989). The biological events within the updated MN zones are fixed at the genus level with an indication of the first and last occurrences of genera, and each MN zone is characterized by a list of main genera (Mein, 1989). However, as Azzaroli (1992) noted, the MN zones lack the flexibility needed for alterations and refinement with the progress of paleontological knowledge. Nonetheless, the MN zones represent a handy tool when dealing with isolated fossiliferous sites that cannot be connected to well-defined stratigraphic sections or are preserved without geological time indication, such as fissure and cave fillings (Schmidt-Kittler, 1989).

The Plio-Pleistocene mammal faunal units of Europe represent a larger-scale biochron system. The Ruscinian (MN14-15) and the Villafranchian (MN16-17) characterize the faunal evolution of Southern Europe during the Pliocene and Early Pleistocene, respectively (Steininger et al., 1989). Rook and Martinez-Navarro (2010) define the Villafranchian as a Mammal Age based on the South European paleontological record, analogous to the mammal ages commonly used in North America. The Villafranchian (from around 3.5 million years ago to about 1.0–1.1 million years ago) is considered a useful tool for large-scale regional and continental chronological correlations (Rook and Martinez-Navarro, 2010). Bellucci et al. (2015) regard the Epivillafrachian (1.2-0.9 million years ago) as a self-contained biochron defining a transitional stage between the Villafranchian and the Galerian. The Galerian Mammal Age, according to Bellucci et al. (2015), includes the faunal units Ponte Galeria, Isernia, and Fontana Ranuccio, ranging from 0.8-0.75 million years ago to around 0.5 million years ago (Gliozzi et al., 1997; Petronio and Sardella, 1999). While the European Plio-Pleistocene Mammal Ages are based on the Italian and French paleontological records, some of them (the Ruscinian and the Villafranchian) are applied to Eastern Europe and Northern Asia as well (Pevzner et al., 1996; Vangengeim et al., 2005, 1998). In the present work, the Ruscinian, the Villafranchian, and the Galerian are used as convenient terms to define the paleobiogeographic affinity of fossil cervid forms, particularly in cases when their exact age or stratigraphic provenance is unknown.

2.7. Conclusions to the Chapter 2

1. The methodological approach employed in this study is based on neontological taxonomic criteria and a rigorous taxonomic revision of fossil cervid taxa, which includes revising type specimens, nominotypical taxa, and nomenclatural acts.

2. The primary objective of this approach is to ensure the taxonomic compatibility of fossil and modern deer taxa. Given the limitations of the fossil record, the applied taxonomic criteria at the genus and species levels tend to follow a "splitting" taxonomy approach.

3. A morpho-functional analysis of diagnostic characters is applied to evaluate their taxonomic value.

4. To determine the systematic position of fossil deer taxa (species and genera) among modern representatives of the family Cervidae, a hierarchical clustering paired group algorithm (UPGMA) was computed using the Jaccard Similarity Index for presence-absence data of diagnostic characters at species, genus, and family levels. This clustering method provides a means to estimate the systematic relationships among the studied taxa.

3. SYSTEMATIC DIVERSITY OF TELEMETACARPAL DEER (SUBFAMILY CAPREOLINAE BROOKES, 1820) IN WESTERN PALEARCTIC

3.1. Subfamily Capreolinae Brookes, 1828

Genus *Lucentia* Azanza and Montoya, 1995

Diagnosis. Small-sized deer with simple two-tined antlers. Pedicles are moderately long, moderately inclined backward and somewhat divergent. Antlers are significantly longer than pedicles, and slender, with a very high position of bifurcation composed of the stronger and longer posterior tine and shorter anterior tine. The antler beam cross-section is irregularly-circular in its proximal section and subtriangular in its distal part. The lateral frontal ridges between the pedicle base and the orbital rim are not developed. The lower fourth premolar is molarized. Lower molars with *Palaeomeryx* fold.

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).

Lucentia iberica Azanza and Montoya, 1995

Diagnosis. A small cervid similar in size to modern European roe deer. The antler beam is bowed in the anteroposterior view with the distal portion pointed medially. The antler bifurcation is situated above the butt at 2/3 of the antler length.

Holotype: the left shed antler MNCN/CR2-S-448 (Azanza and Montoya, 1995: fig. 2) deposited at the Museo Nacional de Ciencias Naturales (Madrid, Spain).

Paratypes: the left partial ramus with P_2-P_4 MPV/CR2-4 (Azanza and Montoya, 1995: figs. 5-3, 5-4) and other specimens (see Azanza and Montoya, 1995) stored at the Paleontological Museum of Valencia.

Locus typicus. Creventille-2 (Alicante Province), Spain.

Stratum typicum. The early Turolian deposits of the Segura-Vinalopo basin at Crevillente-2 (MN 11).

Distribution. Late Miocene, the Iberian Peninsula.

Description. Cranial remains of *L. iberica* are poorly known, resulting in limited information on pedicle morphology. However, some general characteristics have been reported: the pedicles are located at the neurocranial roof behind the orbits, similar to modern cervids. In the better-preserved specimen MPV/CR2-S-30, the pedicle length is longer than 33.5 mm (Azanza and Montoya, 1995).

The antler base is circular, but the antler beam becomes slightly compressed lateromedially soon above the burr. The burr is well-developed and medially inclined to the axis of the proximal part of the beam. The antler beam is slightly compressed anteroposteriorly just above the burr and becomes "semilunar" in cross-section below the ramification. Immediately above the bifurcation, the cross-section of the stronger posterior tine is subtriangular (Azanza and Montoya, 1995: fig. 2). The type antler has a length of 196 mm when measured along the outer curve, with an anteroposterior diameter above the burr of 19.8 mm and a lateromedial diameter of 22.6 mm. The antler ramification is located 125 mm from the burr, and the length of the posterior branch is 71.0 mm. The angle of ramification is acute, varying from 35° to 45° in the Crevillente-2 sample (Azanza and Montoya, 1995). The posterior branch slightly deviates caudally at the level of the antler ramification. The general antler shape exhibits a certain degree of variation in the sample from Creventille-2: antlers may be simply arched with inward curvature, like the type specimen, or lyrated. Young antlers with well-developed burr are simple and unbranched, but in some cases, the trace of further splitting may be recognized in the sharp crest on the anterior side of the distal portion of the antler.

The upper cheek teeth of *L. iberica* are characterized by typical Capreolinae labiolingually narrow crowns (Croitor, 2021). Upper molars may be supplemented with small entostyles and a small protoconal fold, typical for many representatives of the subfamily Capreolinae (Azanza and Montoya, 1995: fig. 4-10). Additionally, upper premolars may evolve additional inner enamel folds on the posterior part of the tooth crown that corresponds to metaconule, and they frequently have a small lingual cingulum (Azanza and Montoya, 1995: figs. 3-22, 4-6). The lower fourth premolar (P_4) is often highly molarized, but this character is variable in *L. iberica*. For instance, P_4 remains unmolarized in the mandibular fragment MPV/CR2-4 (Azanza and Montoya, 1995: figs. 5-3, 5-4)

Lucentia pierensis (Thomas, 1951)

Synonymy:

1951 *Eostyloceros pierensis* sp. nov.: Thomas, p. 256, fig. 1.

Diagnosis. A small-sized deer similar in size to a large *Muntiacus*. Pedicles are long and sloped caudally from the face. Antlers are thin, long, and exceed the length of the pedicle. The height of antler bifurcation in mature individuals equals the length of the pedicle. The posterior branch of antler bifurcation is significantly stronger and longer than the anterior branch and represents a continuation of the main beam. The antler becomes compressed lateromedially in the area of bifurcation and has a sub-rectangular shape of a cross-section. The cross-section of the posterior branch is irregularly circular or ovoid. The lower fourth premolar (P_4) is unmolarized.

Neotype: the fragment of the right frontal bone bearing the almost complete antler IPS/V-22 (Azanza and Montoya, 1995: fig. 6) stored at the Instituto de Paleontologia "M. Crusafont" (Sabadell, Spain).

Locus typicus: Piera, Barcelona province, Spain.

Stratum typicum: „Pontic" deposits of Spain; Lower Turolian, zone MN 11 (Thomas, 1951; Azanza and Montoya, 1995).

Distribution: The Late Miocene of the Iberian Peninsula.

Description. The neotype's frontal bone lacks a bony ridge on the side that connects the base of the pedicle to the posterior side of the orbit rim. The pedicle slopes caudally from the face and is very long, with its anteroposterior diameter making up approximately 30% of its length. The pedicle is 55.4 mm in length, with a distal anteroposterior diameter of 20.2 mm and a lateromedial diameter of 17.3 mm. Its cross-section is oval due to moderate lateromedial compression. The antler measures over 185 mm in length and has a bifurcation point positioned very high above the burr (89.2 mm). The antler's anteroposterior diameter above the burr is 22.0 mm, and the lateromedial diameter is 21.1 mm. The basal segment of the antler has a cylinder shape with an irregularly circular cross-section. At the level of the bifurcation, the antler cross-section has a distinctive sub-rectangular shape. The posterior branch of the bifurcation is longer than the beam segment between the burr and ramification, measuring over 114 mm. This branch continues along the main axis of the antler without curving backward at the level of the ramification. The distal part of the antler curves medially, and the cross-section of the posterior branch is oval or sub-oval. The anterior tine measures 41.8 mm in length, and the angle of ramification is 60° (Azanza and Montoya, 1995).

Genus *Procapreolus* Schlosser, 1924

Diagnosis: Small to medium-sized telemetacarpal deer with commonly three-pointed antlers (up to 5 tines in exceptional cases) characterized by a high position of the first anterior tine (more or less at ½ of the beam length) and a terminal fork oriented more or less in the parasagittal plane. The antler beam is devoid of pearling and tubercles on its proximal part, with a regularly circular cross-section. Pedicles are long (pedicle length measured on the posterolateral side exceeds the pedicle diameter), slightly divergent and sloped backwards from the face, lying in the plane of frontal bones. The distance between pedicles is large: the distance between pedicle bases is ca. two-fold larger than the diameter of the pedicle. The lower premolar series is relatively long: the premolar/molar length ratio varies between 62 and 71%. P_4 is always molarized. Relatively large upper canines are present. Upper molars are supplemented with protoconal fold and hypoconal enamel spur. *Palaeomeryx* fold or its vestige is often present.

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.

Nomenclatural acts. Schlosser (1924) proposed the genus name *Procapreolus* for small-sized deer with three-pointed antlers similar to the roe deer antler structure. Although he did not provide the definition of *Procapreolus*, it can be deduced from the text that the author regards the proposed genus as part of the so-called "*Capreolus* group," which is distinguished from the modern roe deer by the presence of the *Palaeomeryx* fold in the lower molars. Schlosser (1924) originally included three species in *Procapreolus*: *Cervus* (*Palaeaxis*) *loczyi* Pohlig, 1911 from the Late Miocene of Pannonia, *Procapreolus latifrons* Schlosser, 1924, and *Cervavus ruetimeyeri* Schlosser, 1903 (incorrectly spelled as *Cervavus rütmeyeri* in Schlosser, 1924) from the Late Neogene of Mongolia and China.

Korotkevich (1963, 1965b), the first reviewer of the genus, designated *Procapreolus latifrons* as the type species and excluded *Cervavus rutimeyeri* Schlosser 1903 from *Procapreolus* since the shape of its antlers does not correspond to the new diagnosis of the genus. Korotkevich (1963) also attributed dental remains from the Late Tertiary of China described by Schlosser (1903: 118) as *Cervavus* sp. 2 to *Procapreolus*. This cervid form is characterized by primitive lower P_4 (Schlosser, 1903: tab. X, fig. 14) and the presence of a protoconal fold in M^3.

Procapreolus latifrons (estimated body mass of 35 kg) was based on a series of fragmented antlers with a thin beam (diameter approximately 25 mm) and a comparatively high position of the first ramification (approximately 95 mm above the burr). Frontal bones are broad (the breadth of the frontal bone is approximately 45 mm) and flat, and pedicles are compressed anteroposteriorly and relatively long. The beam section is nearly circular, and antler beams are strongly curved outward and backward. The total number of antler tines is unknown because of the fragmented state of fossils (Schlosser, 1924), but the length of a tine may reach 115 mm. Upper canines are large, attaining at least 50 mm in length. P_4 is characterized by advanced molarization, lower molars are supplemented with ectostylids and an anterior "fold of compression." Lower molars are devoid of the *Palaeomeryx* fold (Schlosser, 1924).

Antler remains similar to *Procapreolus latifrons* are not uncommon in the Late Tertiary of China and Mongolia. The proximal fragments of antlers from the Hipparion fauna of China reported by Schlosser (1903: tab. XI, fig. 30) as *Cervus* sp. most probably also belong to *P. latifrons*. The antlered braincase and antler fragments of a small-sized cervid from the *Hipparion* fauna of China figured by Zdansky (1925: Pl. VI, Pl. V, fig. 5) show a great morphological affinity with *Procapreolus latifrons* (Croitor, 2018a). Therefore, *Procapreolus latifrons* is a valid true species, contrary to the opinion of Dong and Ye (1997), and the genus name *Procapreolus* with type species *P. latifrons* should be maintained in the sense proposed by Korotkevich (1963).

Cervavus ruetimeyeri Schlosser, 1903, another Tertiary Asian cervid included by Schlosser (1924) in the genus *Procapreolus*, is based on reportedly somewhat larger upper molars with well-developed basal structures (cingulum?), and the strong inner folding of the hypocone in P^3 and P^4. The lower molars have no *Palaeomeryx* fold (Schlosser, 1903; tab. X, figs. 1-5). The body mass based on dental measurements amounts to 34 kg (Croitor, 2018b), so this species is not distinctly larger than *P. latifrons*. Schlosser (1924) also described some antler remains from the Late Tertiary of Mongolia as *P.* cf. *rütmeyeri* (*sic*!), which is distinguished from *P. latifrons* by the more flattened antler beam, the comparatively lower position of the smaller and weaker first tine, and the stronger posterior tine of distal bifurcation, which should be regarded as the beam continuation. There is a prominent anterior crest between the first tine and the burr, while the posterior side of the beam is flattened, making the transversal section of the proximal part of the beam nearly triangular (Schlosser, 1924). The beam segment between the first and second bifurcations has an irregular cross-section because of the posterior rib and more flattened anterior side of the beam above the basal tine (Schlosser, 1924: fig. 4, B). The antler part in the area of the second ramification is moderately flattened. The antler length is 180 mm, while the burr diameter varies between 25 and 30 mm (Schlosser, 1924). The pedicle has a circular cross-section, with the position on the skull similar to that of the modern *C. capreolus* but relatively longer (Schlosser, 1924). Schlosser (1924) referred to this species having sabre-like upper canines (the length of the largest one attains 42 mm including its root) and some isolated lower molars with the *Palaeomeryx* fold. The upper molars have a large protoconal fold, a weak cingulum (Schlosser, 1924: Pl. IV, figs. 29, 31), and the small entostylids. P_4 is primitive and unmolarised. Korotkevich (1965) observed that *Cervavus rutimeyeri* had distinct antler morphology compared to other members of the genus Procapreolus and suggested that this species should be removed from the genus. I concur with this perspective, as the antler shape of *C. rutimeyeri* closely resembles that of *Pliocervus matheroni*, which lived during the Late Miocene period in France.

The taxonomic status of *Cervus* (*Palaeaxis*) *loczyi* Pohlig, 1911 from the Late Miocene of Hungary remains unclear. The species is based on fragmentary antler remains which are rather poor in quality. The best-preserved shed antler is at least three-tined, with the first tine situated high on the beam, but closer to the burr than to the second ramification. The antler is somewhat compressed from the sides and resembles that of "*Cervavitus novorossiae*". According to Schlosser (1924), the lower molars have a "very distinct" *Palaeomeryx* fold. Pohlig (1911) figured two pedicles, one thin and long, the other short and robust, connected to a small part of the antler. The specimens were collected from various localities and likely belong to different cervid forms. Given the poor quality of the antler remains, the taxonomic status of *Cervus* (*Palaeaxis*) *loczyi* requires further investigation.

Procapreolus moldavicus (Janovskaya, 1954)

Synonymy:

1917 *Cervus sp. juv.*: Khomenko, p. 61
1930 *Capreolus australis* (de Serres): Simionescu, p. 121, figs 51-53.
1930 *Cervus buladensis* (Deperet): Simionescu, p. 121, fig. 58.
1954 *Cervus* (*Rusa*) *moldavicus* n. sp.: Janovskaya, pp. 163-164, fig. 1.
1959 *Procapreolus sp.*: Verestchagin, p.55, fig. 25 (5-6).
1960 *Cervoceros wenzensis* n. sp.: Czyżewska, pl. 2, fig. 2a, pl. 3.
1964 *Procapreolus cusanus* (Croizet and Jobert): Korotkevich, p.383, figs. 1-2.
1964 *Pliocervus sp.*: Korotkevich, p. 385.
1965 *Pliocervus kutchurganicus* sp. n.: Korotkevich, p. 111, fig. 4.
1968 *Procapreolus wenzensis* (Czyżewska): Czyżewska, p. 557.
1970 *Procapreolus sp.*: Korotkevich, p. 110-113, fig. 42.
1999 *Procapreolus moldavicus* (Janovskaya): Croitor, p. 87, figs. 1-4.
1999 *Procapreolus cusanus* (Croizet and Jobert): Croitor, p. 87, fig. 5 c.
2008 *Pliocervus kutchurganicus* (Korotkevich): Vislobokova, p. 300.
2008 *Procapreolus sp.*: Vislobokova, p. 300.

Nomenclatural acts: Janovskaya (1954) suggested that the small-sized deer from the Pliocene of Moldova represented a transitional evolutionary stage between the Late Miocene *Cervavitus* and the modern genus *Cervus*. Croitor (1999) included this species in the genus *Procapreolus* and synonymized *Procapreolus* moldavicus with *Cervocerus wenzensis* Czyżewska, 1960 from the Early Pliocene of Węże-1 (Poland).

The poorly preserved antlers from the Early Pliocene of Kuchurgan, which Korotkevich (1965) described as *Pliocervus kutchurganicus*, fall within the range of individual variation of the sample from Węże-1, and therefore *Pliocervus kutchurganicus* is regarded as a junior synonym of *P. moldavicus* (Croitor and Stefaniak, 2009). While some antlers from Kuchurgan were reported by Korotkevich (1970) as *P.* cf. *cusanus*, the author failed to demonstrate the presence of two species in the dental and postcranial material from Kuchurgan.

This taxonomic confusion between *Procapreolus* and *Pliocervus* is due to the poor and vague definition of the type species of the genus *Pliocervus*, *Cervus matheroni* Gervais, 1859 from the Late Miocene of France (Croitor, 2014). In contrast to *Procapreolus*, *Pliocervus matheroni* is characterized by massive pedicles with more or less parallel orientation, and a small distance between them, as in *Capreolus*, differing from the broad-spaced pedicles of *Procapreolus*. The fully developed antlers of *P. matheroni* are four-pointed with an irregular subtriangular cross-section of the beam and triangular cross-section of tines, unlike the regularly circular cross-sections of the beam and tines in most *Procapreolus* species, or oval cross-sections of flattened tines in *P. cusanus*. None of the antlers from Kuchurgan corresponds to the diagnostic characters of *Pliocervus*. Finally, the lower fourth premolar (P_4) of *P. matheroni* is primitive, unlike the highly molarized P_4 in *Procapreolus* (Croitor, 2014).

According to Vislobokova (2008), the taxonomic status of *Cervus* (*Rusa*) *moldavicus* is doubtful due to the type specimen being a juvenile female, which lacks diagnostic characteristics such as antler morphology and permanent premolar morphology. Vislobokova (2008) suggests considering Janovskaya's deer as *Procapreolus* sp. and using *Procapreolus wenzensis* (Czyżewska, 1960) to identify the archaic capreoline deer from Eastern Europe during the Early Pliocene. Vislobokova (2008) also supports the validity of *Pliocervus kuchurganicus* Korotkevich, 1965 and mentions *P. cusanus* (Croizet and Jobert, 1828) as part of the fauna from Kuchurgan.

The debate on the priority of scientific names initiated by Vislobokova (2008) is unnecessary as fossil remains from Węże-1 also contain cranial remains of juvenile females, including the fine skull Nr. 345 chosen as a paratype of *Cervoceros wenzensis* by Czyżewska (1960), which are morphologically identical to the holotype of *P. moldavicus* (Croitor and Stefaniak, 2009). While antler morphology is not diagnostically important for defining species in this case, as antlers within the genus *Procapreolus* are uniform and do not provide secure diagnostic characters except for fully developed antlers of *P. cusanus*, species of the genus *Procapreolus* can be distinguished by details of dental morphology, such as the development of *Palaeomeryx* fold in lower molars and the presence of cingulum in upper molars (Korotkevich, 1970, 1974). The upper and lower molars of the holotype of *P. moldavicus* provide the necessary diagnostic characteristics for species definition and ensure differential diagnosis.

Diagnosis: The species size is close to the body size of modern hog deer or slightly larger. The frontal-orbital part of the skull is short: the anterior edge of the orbits is situated above M^2. Frontal bones are flattened, with sharp supraorbital channels ranging from the pedicle base to the level of preorbital fossae. The preorbital fossa is very large: the diameter of the preorbital fossa in males attains ca. 74% of the orbital diameter; the ethmoidal openings are large: their length equals the diameter of orbits. The intermaxillary bones are narrow and pointed. The mandibular diastema is relatively short (shorter than in *Capreolus*). The nasal bones are short and do not reach the line connecting the anterior edges of the orbits.

The fourth lower premolar (P_4) is characterized by a high degree of molarization; the lower molars have a *Palaeomeryx* fold, which may be variable. The upper molars are supplemented with protoconal and hypoconal folds, the cingulum is reduced and normally not visible. Upper canines in males are moderately large.

The antlers are three-pointed, thin, and lyre-shaped; the first tine is located very high on the anterior side of the beam. The antlers may be flattened in the area of ramifications, however, the antler beam between the first and second ramifications is never flattened.

Holotype: the holotype of *Cervus* (*Rusa*) *moldavicus* is a partial articulated skeleton of a juvenile female (No. 2), which includes the skull, mandible, backbone, ribs, os innominatum, and posterior limbs. The specimen is currently stored in the collection of the Paleontological Institute of the Russian Academy of Sciences in Moscow. Unfortunately, the braincase of the skull (Nr. 2/1) is heavily damaged, with only the parietals and the right temporal bones preserved (Fig. A.1). Additionally, the left side of the face is also damaged, with the contact of both premaxillary bones with the rest of the skull not preserved.

To reconstruct the orbitofrontal part of the skull, plaster was used, which resulted in an imperfect reconstruction. The flexion of the skull (the angle between the facial and cerebral parts) was not maintained, and the orbitofrontal part was artificially lengthened due to the two parts of the preserved right zygomatic arch not coinciding. The gap between them is approximately 13 mm, and the axis of the braincase is noticeably offset leftward (Croitor, 1999).

The upper molars of the holotype are characterized by the presence of a large protoconal fold, a hypoconal spur, and a well-developed flat entostyle, which extends into a weak cingulum. These characteristics are also present in PD^4 of the holotype (Janovskaya, 1954: fig. 3). The lower molars are characterized by the presence of a well-developed ectostylid and a *Palaeomeryx* fold (Janovskaya, 1954: fig. 5).

Type locality: “Cahul River valley, Fagadil village” (Janovskaya, 1954); nowadays this site is situated in the southern part of Lebedenco village (= Fagadyl: Khomenko, 1917; Croitor, 1999; Vislobokova, 2008; = Făgădău: Eremia, 2011), Cahul District, Moldova. To be more precise, the present-day Lebedenco village is a composite of two previously separate settlements, namely Crihana Veche and Făgădău. The latter locality today is the southern part of Lebedenco village (Eremia, 2011).

Stratum typicum: the "Middle Pliocene" (Janovskaya, 1954); the Early Pliocene, MN15, Carbolian alluvium.

Distribution: Early Pliocene (MN14-15) of Poland, Ukraine, Moldova, and Romania (Khomenko, 1917; Janovskaya, 1954; Croitor, 1999; Vislobokova, 2008).

Description. The studied cervid has a similar body mass to the hog-deer, estimated at approximately 40-50 kg. The type specimen exhibits a preorbital fossa, which is notably deep and relatively large, measuring approximately 1 cm in depth and 21.0 × 12.0 mm in size. The dentition of this specimen includes fully functional deciduous teeth, as well as functional first and second upper and lower molars, with the third molars in the process of eruption. Additional measurements obtained are as follows: skull breadth at PD^4, 66.0 mm; skull breadth at PD^2, 35.2 mm; skull breadth at M^2, 34.0 mm; palatal breadth between M^2, 34.0 mm; length of right upper tooth row (PD^2-M^3), 70.4 mm; length of right upper molars (M^1-M^2), 41.5 mm; and length of right upper deciduous teeth (PD^2-PD^4), 34.2 mm. The overall proportions of the cranium reveal a short orbitofrontal area, with the anterior edge of the orbits positioned above M^2, similar to that of modern *Muntiacus*, *Capreolus*, and *Odocoileus*. The frontal bones in *P. moldavicus* are rather flat compared to those of modern roe deer, exhibiting a slightly depressed frontal profile above the orbits and convex in front of the pedicles. Furthermore, the pedicles in *P. moldavicus* are remarkably long, with a length always greater than the pedicle diameter. They are sloped backwards from the face at an angle of about 50°, and oriented slightly laterally, resulting in an angle of approximately 30° between the pedicles. The nasal bones in the male skull Nr. 220 from Węże-1 and the female skull from Fagadâl are relatively short, resembling those of *Odocoileus* and *Muntiacus*, and do not reach the level of the orbits, as in *Capreolus*. The premaxillary bones are articulated with the nasal bones, as indicated in the skull Nr. 220 from Węże-1 (Fig. A.2) and the skull from Fagadâl.

Sexual dimorphism is evident in the size and shape of both the preorbital fossae (preorbital pits) and the supraorbital channels. The supraorbital channels are long, deep, and sharply defined, beginning at the base of the pedicle and extending to a level above the preorbital fossae. In males, the supraorbital openings are situated within these channels and are larger and more developed than those in females. The length of the supraorbital channel in specimen Nr. 220 from Węże-1 measures 58 mm, while in the female skull Nr. 345, it is only 37 mm long and weaker in appearance. This channel is more pronounced and has a parallel orientation to the interfrontal suture compared to those in *Capreolus* and Pliocene *Pavlodaria* from Kazakhstan.

In males, the preorbital fossae are triangular with sharp edges and are notably large, deep, and extend up to 29 mm in length, 24 mm in height, and 10.4 mm in depth in the male skull from

Węże-1. Conversely, in females, the preorbital fossae are smaller, deep, and rounded, measuring 27×14.5 mm in the female skull Nr. 345 from Węże-1 and 21×12 mm in the female from Fagadâl, with a depth of 10 mm in the latter specimen. The relative length of the preorbital fossa to the diameter of the orbit in male *P. moldavicus* (74.4 %) is somewhat smaller than in *Muntiacus*. Among the modern *Muntiacus* deer, the smallest preorbital fossa is recorded for *M. muntjak* (with a relative length to orbit diameter of 81.4 %), while the largest preorbital fossa is observed in M. reevesi (with a relative length to orbit diameter of 99 %) (Ma et al., 1986)

Male *P. moldavicus* have relatively large upper canines. In the male skull Nr. 220, the anteroposterior diameter of the right canine alveolus is 6.2 mm, and the distance between the canine and P^2 is 35.4 mm. The length ratio between lower premolars and molars in the Węże-1 sample varies from 62.6% to 65.7% (n=4). However, in the specimen from Musait (Moldova), the lower premolar series is relatively long, with the premolar/molar length ratio amounting to 70.6%.

The upper molars in *P. moldavicus* have a large protoconal fold and a hypoconal spur, similar to those of modern *Odocoileus virginianus*. The lingual side of the molars is strongly inclined, with the angle between the labial and lingual sides of the upper molar measuring 55°. The entostyle, a ridge on the lingual surface of the molars, is variable in *P. moldavicus*. It is well developed in the type specimen from Fagadâl and in the isolated M^{1-2} from Tatareşti, Moldova (Nr. 77, IZC; see Fig. A.3), but completely reduced in the majority of specimens from Węże-1. The entostyle is only found in two specimens of the sample: in the isolated tooth without number and in the upper tooth-row Nr. 294.

The lingual wall of P^2 lacks a vertical groove and is not cleft. Its hypocone is supplemented by an internal enamel fold, and the rib of the paracone is stronger than that of *C. capreolus*. P^3's lingual side is grooved, and its hypocone features an internal enamel fold that may disappear in heavily worn teeth. Additional internal enamel folds may occur in both the protocone and hypocone of P^4, which may also disappear in advanced stages of wear.

Lower molars are characterized by the development of ectostylids. The *Palaeomeryx* fold is rather variable: it is well expressed in the holotype from Fagadâl but quite poorly developed in the lower mandible from Musait (Croitor, 1999). The variation in *Palaeomeryx* fold development is observed in the Węże-1 sample. The *Palaeomeryx* fold is represented by a weak vestige in specimen Nr. 220, but it is present in 69% of the specimens in the sample (11 of 16 specimens). *Palaeomeryx* fold is stronger and more often developed in M_1. The development of ectostylids in M_3 is also variable. M_3 may have both anterior and posterior ectostylids (e.g. specimen Nr. 248, IZW), or possess only the anterior ectostylid as in the specimen Nr. 220 from Węże-1.

The morphology of the P_4 tooth in *Procapreolus* is consistent and does not display significant individual variation. The parastylid is reduced and the metaconid is fused with the paraconid, though it does not connect with the protoconid, leaving the anterior valley incompletely isolated. The entoconid is not connected to the entostylid. The length of the lower premolar series is about 70% of the molar series length.

The antlers of *Procapreolus* are always three-pointed, long, and thin, with a straight or undulating beam at the base. The basal portion of the antler beam has a circular transverse section, though it can become somewhat compressed distally, with a flat lateral side and a convex medial side. The antler is highly compressed lateromedially in the areas of the first and second bifurcations, but the beam segment between the first and second ramifications is never flattened. The first tine is located very high, almost halfway up the antler's length, and is short in young individuals but much longer in fully developed antlers. The antler surface is ornamented with ridges and furrows.

The antler series from the Węże-1 site is interesting because it demonstrates the range of variation in a homogenous sample. For example, the antlers of specimen Nr. 220 (IZW) are thin, with the antler base inclined backward from the burr and then curved toward the anterior and sides, reminiscent of the "S-shaped" morphology of "*Pliocervus kutchurganicus*". The antler becomes compressed lateromedially in the area of the first tine, and the antler beam has a deep groove on the anterior side that continues onto the anterior side of the first tine. The transverse section of the beam above the first tine is circular. The distal portion of fully developed antlers is significantly compressed from the sides in the area of the distal bifurcation, as seen in specimens W-328 and W-329. In comparison, the proximal antler fragments Nr. 324 (DLM above burr is 26.5 mm) and Nr. 364 (measurements are unavailable) are somewhat more robust and straight, unlike specimen Nr. 220 (DLM above burr is 22.0 mm). Thus, the type specimen of "*Pliocervus kutchurganicus*" (DLM above burr amounts to 31.2 mm) represents a variant of antler shape also found in the sample from Węże-1, while the size of antlers from the Polish sample falls within the size range of antlers from Kuchurgan described by Korotkevich (1970) as "*Pliocervus kutchurganicus*" (DLM above burr: 13.3-31.2 mm).

Recent research suggests that the fine pair of antlers found at the Pliocene site of Czorna Losczina in South Ukraine, previously identified by Korotkevich (1964) as *P. cusanus*, and the complete antler (Nr. 33-169, IZU) with two mandibles (Nrs. 33-160, 33-161, IZU) from Andreevka (Ukraine), previously reported by Korotkevich (1970) as *P. cf. cusanus*, actually belong to *P. moldavicus*. This conclusion is based on comparisons of postcranial measurements of the holotype from Fagadâl (Moldova) and the postcranial fragments from Węże-1 (Poland) and

Maluşteni (Romania), which do not show any significant differences and fall within the variation range of the species (Croitor and Stefaniak, 2009).

Interestingly, the femur of *P. moldavicus* is relatively long for the thoracolumbar portion of the backbone, with a ratio of 38.7%, compared to the open-landscape adapted tundra reindeer, whose femur is only 34.5% relative to the backbone, and the dense forest dweller *Muntiacus muntjak*, whose femur is 35.1%. These proportions suggest that *P. moldavicus* was adapted to the saltatorial type of locomotion in the conditions of forest and woodland habitats, similar to modern deer. Thus, the general proportions of the postcranial skeleton of *P. moldavicus* seem to be close to modern deer adapted to forest and woodland habitats (Croitor 1999).

Procapreolus pentelici (Dames, 1883)

Synonymy:

1862 *Dremotherium sp.*: Gaudry, p. 308.
1867 *Dremotherium sp.*: Gaudry, pl. LVI, fig. 7.
1883 *Cervus pentelici* nov. sp.: Dames, p. 93, pl. V, fig. 1.
1898 *Capreolus pentelici* (Gaudry): Trouessart, p. 889.
1968 *Pliocervus pentelici* (Caudry): Melentis, p. 4, pls. 4-5.
1995 *Pliocervus graecus* n. sp.: Azanza, p. 158, pl. 1, fig. 2.
2017 *Procapreolus cusanus* (Croizet and Jobert): Cregut-Bonneure and Tsoukala, fig. 7.

Nomenclatural acts. Dames (1883) described a new species, *Cervus pentelici*, from Pikermi (Greece) based on a well-preserved pair of three-pointed antlers and associated them with a braincase without cranial appendages and mandible of small-sized cervid and a mandible of a larger deer previously described by Gaudry (1862, 1867) as *Dremotherium pentelici* and *Dremotherium* sp. respectively. The obvious difference between relative dental size and the relatively large size of antlers was attributed by Dames (1883) to sexual dimorphism. Gaudry (1862, 1873), who studied both samples from Pikermi and Mont Luberon, did not report the similarity between Greek and French cervid remains.

Subsequent revision of the material revealed that the smaller mandible (PIK2034a, *sin*; PIK2034b, *dx*; MNHN, Paris) from Pikermi described as *Dremotherium pentelici* belongs to a muntjac-sized ruminant (L P_2-M_3 amounts to 55.4 and 55.0 mm respectively), while the braincase PIK2020 (MNHN) does not belong to a deer; the collection label associated with the specimen defines it as "*Gazella brevicornis* cf. *capricornis*/*deperdita*?". Melentis (1969) included the material described by Gaudry (1862, 1873) and Dames (1883) in Gaudry's species, which was placed in the genus *Pliocervus*. Azanza (1995) reports a great similarity between the antlers from Maramena and those from Pikermi and confirmed the presence of the second smaller cervid in the fauna from Pikermi that should maintain the species name given by Gaudry: *Dremotherium* *pentelici*. Azanza (1995) established a new species name, *Pliocervus graecus*, for a larger cervid form to avoid the homonymy of species names proposed by Gaudry (1862) and Dames (1883). Species name *Cervus pentelici* Dames, 1883, however, remains available for the larger cervid from Pikermi characterized by three-tined antlers and is not a homonym of *Dremotherium pentelici* Gaudry, 1862, since those two species' names were originally established in combination with different generic names (ICZN, Article 53.3), and the secondary homonymy is improbable. Therefore, *Cervus pentelici* Dames, 1883, is a senior synonym of *Pliocervus graecus* Azanza, 1995.

Holotype: a pair of antlers 1967/18 of an adult individual stored in the paleontological collection of the University of Athens (Dames, 1883; Melentis, 1969).

Type locality: Pikermi, Greece.

Stratum typicum: Late Miocene, Turolian, the boundary of MN12/MN13.

Emended diagnosis: The body size is similar to modern European roe deer. Antlers are thin, three-pointed, with circular cross-sections of the beam. The first tine is situated closer to the distal bifurcation than to the burr. Pedicles are very long: their length measured from the posterolateral side significantly exceeds the diameter of the pedicle. The *Palaeomeryx* fold in the lower molars is not present. The cingulum in the upper molars is not developed.

Description. The morphological characteristics of the deer from Pikermi and Maramena are consistent with the genus *Procapreolus*. The antlers of the deer have three tines and are thin, long (390 mm), and have a very high position of the first tine. The beam has a circular cross-section, while the pedicles are thin and slightly diverging, with a large distance between them. Furthermore, P^4 is highly molarised, unlike in *Pliocervus matheroni*, where it is simple. The body size of *P. graecus* is 27 kg, which is very close to that of *P. florovi*. However, unlike the latter species, the Greek cervid lacks a *Palaeomeryx* fold in the lower molars. In addition, the lingual wall of upper premolars is split by a deep vertical groove, which is more pronounced than in *P. moldavicus* from Weże. While *P. graecus* is very close to *P. florovi*, it has somewhat more advanced dental morphology.

Cregut-Bonnoure and Tsoukala (2017) reported capreoline remains from the younger Pliocene site of Gephyira (Greece) as *P. cusanus*. These remains are characterized by a size similar to *P. pentelici* and *P. cusanus* and, like those two species, lack a *Palaeomeryx* fold. However, unlike *P. cusanus*, the antlers of the deer from Gephyra are thin and not flattened in their distal part. Despite its significantly younger age (MN16a), *Procapreolus* from Gephyra is closer to *P. pentelici* than to *P. cusanus*.

Procapreolus vesti (Korotkevich, 1970)

Synonymy:

1959 *Procapreolus sp.*: Verestchagin, p. 52, figs. 25-5, 25-6.
1959 *Pliocervus sp.*: Verestchagin, p. 52.
1970 *Pliocervus kutchurganicus vesti* ssp. nov.: Korotkevich, p. 133, fig. 48.
1970 *Procapreolus sp.*: Korotkevich, p. 109, fig. 41.
2009 *Procapreolus moldavicus* (Janovskaya, 1954): Croitor and Stefaniak, p. 17, fig. 13-b.

Nomenclatual acts. Verestchagin (1959) described a well-preserved shed antler and lower mandible from Kosyakino as *Procapreolus* sp. In the same publication, Verestchagin (1959) listed *Pliocervus* sp. in the faunal inventory of Kosyakino, but did not provide any specific fossil material confirming the presence of this genus. Subsequently, Korotkevich (1964) suggested that the material figured by Verestchagin belongs to *Pliocervus*. Later, Korotkevich (1970) described a new subspecies *Pliocervus kutchurganicus vesti* based on a well-preserved antler from Kosyakino that belonged to a mature individual. In the same work, Korotkevich (1970) identified a very thin antler from Kosiakono with a rather short first tine situated at an almost equal distance between the burr and the distal bifurcation as *Procapreolus* sp., correctly interpreted as belonging to a young animal. Croitor and Stefaniak (2009) suggested that the material from Kosyakino may belong to *P. moldavicus*. However, the small body size similar to that of modern muntjacs indicates that the material represents a true species of *Procapreolus* that is adapted to a specific ecological niche.

Holotype: the almost complete right antler with pedicle and part of frontal bone Nr. 1 (Fig. 3.4 A) stored in the Zoological Institute, Sankt-Petersburg (Korotkevich, 1970).

Type locality: Kosiakinsky Quarry (= Kosiakino: Pevzner et al., 1996) near Stavropol, Russia.

Stratum typicum: Pliocene (MN 15?).

Distribution. Pliocene of North Caucasus foothills (Russia). According to Verestchagin (1959), the fauna from the alluvial sands of Kosiakinsky Quarry is close to the fauna from Malușteni (Romania). Pevzner et al. (1996) indicate the mixed character of the fossil remains from this site.

Diagnosis. The body size is comparable to modern muntjacs. Antlers are relatively large, three-pointed, with rounded cross-sections of beam and tines. The antler segment between the first and second ramifications often is elongated. Lower molars are with *Palaeomeryx* fold. Upper molars are devoid of the cingulum.

Description. The type antler is relatively robust (DLM antler base is 28.4 mm) and belongs to a mature individual. The first ramification is situated approximatively in the middle between the burr and the second ramification (L burr - ramification amounts to 108.4 mm; L first - second ramifications amounts to 118.0 mm). The cross-section of the antler beam is regularly circular. The pedicle is relatively long (L – 32.0 mm; DLM – 25.6 mm) and slightly compressed anteroposteriorly (DAP – 24.9 mm). The frontal bone has a rather deep, well-outlined and long supraorbital channel.

P. vesti is the smallest species of the genus (L P_2-M_3 = 58.0 – 73.0 mm; n=3; the estimated mean body mass amounts to 21.5 kg) that represents a particular direction of specialization within *Procapreolus*. Besides the small body size, *P. vesti* also is characterized by a relatively longer antler segment between the first and second ramifications, although the antler proportions of *P. vesti* broadly overlap with *P. cusanus*. All dental remains from Kosiakino are characterized by molarized P_4 and the presence of *Palaeomeryx* fold in lower molars (Korotkevich, 1970). Korotkevich (1970) reports the morphological heterogeneity of the sample from Kosiakinsky Quarry and distinguished larger teeth with stronger *Palaeomeryx* fold that she described as *Procapreolus*, and smaller teeth with weak *Palaeomeryx* fold that, according to Korotkevich, belong to *Pliocervus*. The observed size and morphological variation correspond to the intraspecific variation and, most probably, confirm the fact that the sample from Kosiakino chronologically is not homogenous.

Procapreolus cusanus (Croizet and Jobert, 1828)

Original description: *Cervus cusanus* Croizet and Jobert (1828: Pl. III, figs. 1, 2 ; « Cerfs fossiles de la montagle de Perrier (second sous-genre). »).

Nomenclatural acts: The initial mention of the species name *Cervus cusanus* can be traced back to the bibliographic notes in Croized and Jobert’s (1828) volume on fossil remains from the Department Puy-de-Dôme, which also features an illustration of a complete right antler with frontal and parietal bones (Croized and Jobert, 1828: Pl. VIII, figs. 1-2). Although the second volume of Croizet and Jobert's work, containing a description of the species, was not subsequently published (Heintz, 1970), the first official description of *Cervus cusanus* Croizet and Jobert was presented by Pomel (1853), who also proposed definitions for the new species *Cervus leptocerus*, *Cervus platycerus*, and *Cervus furcifer*. These species share the same size and antler bauplan as *C. cusanus*, differing only in minor morphological details, which Heintz (1970) regarded as individual variants of the same species. Depéret (1884), on the other hand, proposed the new species name *Cervus neschersensis* for a smaller cervid from Ravine Les Etouaires characterized by more flattened antlers with a comparatively lower position of the first tine. The measurements of a mandible attributed by Depéret (1884) to *Cervus neschersensis* correspond to those of the specimen PET809 from MNHN in Paris. Heintz (1970) demonstrated that all the species described by Pomel (1853) and Depéret (1884) fall within the range of variation of *Cervus cusanus*. Additionally, Heintz (1970) notes that the collection studied by Croized and Jobert (1828) does not include any antler that matches the original illustration with absolute precision. It is possible that the antler designated by Heintz (1970) as a neotype is the specimen figured by Croizet and Jobert (1828).

Korotkevich (1963, 1970) placed *Cervus cusanus* Croizet and Jobert, 1928 in *Procapreolus*. Valli (2010) confirmed that *P. cusanus* belongs to telemetacarpal cervids, as it exhibits a characteristic for capreolinae shape of the post-glenoid foramen, which is not surrounded by squamosal bone and is bordered in its posteromedial section by the petrous bone.

Diagnosis and synonymy: see Heintz (1970: p. 68).

Differential diagnosis: The species is distinguished from other species of the genus by its flattened antlers and by the presence of supernumerary antler tines (up to 5 tines in total). Its lower molars are devoid of *Palaeomeryx* fold, unlike *P. ucrainica*, *P. flerovi*, *P. vesti*, and *P. moldavicus*. The species is distinguished also by its smaller size from *P. moldavicus* and by the absent lingual cingulum in upper molars from *P. ucrainicus*.

Neotype: a right antler with pedicle and frontal bone lacking the tip of posterior tine of the distal fork (Fig. 3.4 B).

Distribution: Ravine Les Etouaires (type locality; =Perrier-Etouaires, = Boulades: Deperet 1884), Issoire, France (Heintz, 1970); alluvium of Etouaires, Late Pliocene (Early Villafranchian). Remains of this deer are reported from the Pliocene of France, Italy, and England (Heintz, 1970; Abbazzi et al., 1995; Lister, 1999).

Description. *P. cusanus* is the most advanced species of the genus to have survived into the Early Villafranchian of Western Europe. It is a relatively small-sized species with an estimated body mass of approximately 30 kg. This species is characterized by advanced antler morphology and dentition, which lack archaic enamel folds (the *Palaeomeryx* fold) and basal structures (cingulum). The antlers of *P. cusanus* feature a flattened extension in their distal parts, which become highly pronounced in adult males (Heintz 1970). The beam segment between the first and second ramifications of *P. cusanus* is distinctly flattened, which is a reliable distinguishing feature from other species of *Procapreolus* that may have flat extensions in the area of the ramifications, but their beam between ramifications remains generally cylindrical. The position of the first tine is quite variable, with the height of the first ramification ranging from 63 to 145 mm (n=7). The length of the second segment is also variable, but appears to be comparatively longer than in other species of the genus (70 – 110 mm; n=4). The extreme range of variability of the height of the first tine insertion may be due to the larger sample of antler remains compared to other species of the genus. Mature antlers of *P. cusanus* may bear up to five tines, an exceptional case among species of the genus *Procapreolus* characterized by uniformly three-tined antlers.

All available specimens show advanced molarization of the P_4, with the metaconid fused to the paraconid (Fig. A.5); the posterior wing of the metaconid may be weak or absent. The premolar/molar ratio is approximately 69%, consistent with the general dental row proportions observed in the genus. Upper molars display a protoconal fold and hypoconal spur, while a true cingulum is never present. Heintz (1970) describes anterior and posterior enamel "folds of compression" as possible remnants of the cingulum

Our knowledge of the cranial remains of *P. cusanus* is limited. The only known antlered braincase of this species is the type specimen of Deperet's *Cervus buladensis*, which belongs to a young individual (see Table A.1). The pedicles of this specimen are relatively long, with a circular cross-section, and are almost parallel to each other. They are strongly sloped back from the face, a characteristic seen in modern *Muntiacus*. Notably, the space between the pedicles is larger than in modern *Capreolus*.

The parietal bones exhibit a slight convexity, and the lambdoid suture takes on an M-shape. The bullae tympani are compressed and relatively small. In comparison to a braincase from Gephyra, Greece identified by Cregut-Bonnoure and Tsoukala (2017: fig. 7) as *P. cusanus*, the frontal bones are relatively narrow for the braincase breadth, with a frontal breadth to braincase breadth ratio of 90.0%. It is possible that the relatively narrow frontal bones are linked to the young age of the specimen from Etouaires.

Procapreolus pyrenaicus (Depéret, 1890)

Synonymy:

1890 *Cervus ramosus pyrenaicus* Dep.: Depéret, p. 124.
2000 *Croizetoceros pyrenaicus* (Depéret): Azanza, p. 212.
2018 *Procapreolus pyrenaicus* (Depéret): Croitor, p. 34.

Nomenclatural acts: Deperet (1890) initially identified *Cervus ramosus pyrenaicus* from the Early Pliocene of Roussillon (France) as a transitional evolutionary stage between *Pliocervus* matheroni and *Croizetoceros ramosus*. However, according to Heintz (1970) and Dong (1996), the antler morphology of "*C.*" *pyrenaicus* is distinct from *Croizetoceros ramosus* due to fundamental differences in their bauplan. The antlers of "*C.*" *pyrenaicus* are characterized by the first short ramification's high position, which forms an acute angle with the beam, while the second tine is located on the posterior side of the beam, in contrast to *Croizetoceros* (Depéret, 1890: pl. VIII, fig. 3; Heintz, 1970: 57, fig. 102; Dong, 1996: pl. 2, fig. 3). Moreover, the antler beam of "*C.*" *pyrenaicus* becomes somewhat flattened above the first ramification. P_4 exhibits a trend toward molarization (Dong, 1996). Dong (1996) suggests that the antlers of "*C.*" *pyrenaicus* resemble those of *Procapreolus*, a viewpoint supported in this study

Diagnosis: Antlers are thin, long, and three-pointed. Pedicles are moderately long: pedicle length roughly equals pedicle diameter. The antler base is circular; antlers become laterally compressed in the area of the first ramification. The antler segment between the first and second ramifications is also compressed from the sides, however, the distal part of the antler is not palmed.

Lectotype: antlered frontlet (Deperet, 1890: pl. VIII, fig. 3).

Description. The basal segment of the antler between the burr and the first ramification is cylindrical in shape. The antler is compressed from the sides in the area of the first ramification and remains compressed until the second ramification. The first tine is cone-shaped, while the distal tines show moderate lateral compression. However, the distal portion of the antlers of *P. pyrenaicus* does not form a broad flattening as in *P. cusanus*. Deperet (1890: pl. VII, fig. 6) assigned to this species a right mandibular ramus with a primitive, unmolarized P*4*, and devoid of the *Paleomeryx* fold molars. The attribution of this specimen to *P. pyrenaicus* is uncertain. The estimated body mass is around 35 kg.

Distribution: Early Pliocene of Roussillon, France.

Procapreolus ucrainicus Korotkevich, 1963

Synonymy:

1963 *Procapreolus ucrainica sp. nov.*: Korotkevich, p. 1390, fig. p. 1391.
1965 *Procapreolus ukrainicus sp. nov.*: Korotkevich, p. 62, figs. 1-3 (unjustified emendation).
1970 *Procapreolus ucrainicus* (Korotkevich): Korotkevich, p. 72.

Nomenclatural acts: The species name *Procapreolus ucrainica* was proposed in a brief publication by Korotkevich (1963). The new species description was illustrated by a figure of antlers from Novoukrainka (one larger specimen with broken tines and two smaller antlers belonging to a juvenile individual) and a comparison with Pliocene cervid remains from Eastern Europe reported as *P. cusanus*. According to Article 34.2 of ICZN, the Latinized adjectival *ucrainica* should be changed to *ucrainicus* to be in accordance with the generic name *Procapreolus*.

Later, Kotorkevich (1965a) proposed a new species name, *P. ukrainicus*, based on a series of antlers and teeth: the larger antler Nr. 38-184 and the juvenile antler Nr. 38-182, which were already figured in Korotkevich (1963), the upper tooth series M^2-M^3 Nr. 38-420, and the lower tooth series M_2-M_3 Nr. 38-421. All material comes from Novoukrainka and is designated by Korotkevich (1965a) as the holotypes (*sic*!) of *Procapreolus ukrainicus*. The species name *P.*

ukrainicus is an unjustified emendation (ICZN, Article 33.2.3.), which is not in prevailing usage since this name is frequently spelled as *P. ucrainicus* Kotorkevich, 1965 (Korotkevich, 1970). The antlers figured in Korotkevich (1963) are syntypes of *P. ucrainicus*, while the additional dental material proposed as "holotypes" of *P. ukrainicus* cannot be considered as syntypes of *P. ucrainicus*.

Diagnosis: Body size as in modern European *Capreolus capreolus*. The position of the first ramification is higher than in other species of the genus: the distance between the burr and the first ramification is longer than the distance between the first and second ramifications. The antler beam is cylinder-shaped. Pedicles are long: their length is always longer than the diameter. Upper molars with well-developed cingulum; lower molars with *Palaeomeryx* fold.

Syntypes: Right antler with a pedicle of adult individual Nr. Nr. 38-184, juvenile right antler with pedicle Nr. 38-182, juvenile left antler with pedicle Nr. 38-183. The material is stored in the Natural History Museum of Kyiv (Ukraine).

Locus typicus: Novoukrainka (=Novo-Ukrainka, =Budionovka), Odesa region, Ukraine.

Stratum typicum: Late Miocene (Maeotian), MN11-12.

Distribution: Late Miocene, Europe (Ukraine, Italy).

Description: This is the most primitive species of the genus, characterized by long and thin three-tined antlers without pearling in their proximal portions. The antlers are lyre-shaped, with the parallel lower portion of antler beams or becoming divergent immediately above the burr (angle of deviation from the pedicle axis amounts to 20-30^0). The position of the first tine is very high, closer to the distal bifurcation than to the burr. Compared to other species of the genus (*P. vesti* and *P. cusanus*), this species is characterized by the generally shortest second segment of the antler. Pedicles are relatively long, being the longest within the genus, and strongly sloped backwards from the face. The transverse sections of the pedicles and the lower part of the beam are regularly circular.

The dental morphology of *P. ucrainica* is the most primitive among the European *Procapreolus*. Upper molars are brachyodont with a significantly sloped lingual wall (angle between lingual wall and crown base amounts to 40-45^0) supplemented with a well-developed cingulum, protoconal fold, and large and complicated hypoconal spur. Lower molars show a well-developed *Palaeomeryx* fold (Korotkevich, 1963, 1965a). The premolar/molar ratio of the only known complete lower mandible (Nr. 38-374) amounts to 65.4% and is situated in the lower part of the variation range of this characteristic in the genus *Procapreolus*. The body mass estimation based on the dental remains series amounts to 32 kg, and the body mass based on the largest specimen attains 38 kg.

The remains of a small-sized cervid from the Late Miocene of Bacinello (Italy) reported by Abbazzi (2001) as *P.* cf. *loczyi* also belong to *P. ucrainicus*. The Italian material demonstrates such important diagnostic characteristics as cingulum in upper molars and Palaeomeryx fold in lower molars.

Procapreolus florovi Korotkevich, 1974

Diagnosis: Body size as in modern European roe deer. Upper molars are devoid of the cingulum. The *Palaeomeryx* folder in the lower molars is very weak.

Holotype: the antlered frontoparietal fragment of skull Nr. 45-26306

Locus typicus: left shore of the Hadjibey Lake, Cherevychnyi Village, Odesa Region (Ukraine).

Stratum typicum: Late Miocene (end of Maeotis), MN12.

Description. *P. florovi* is a small-sized species from the final Miocene of Ukraine, estimated to have a body mass of 30 kg. Like the previous species, it has long and thin three-pointed antlers. *P. florovi* is characterized by relatively and absolutely longer pedicles compared to other *Procapreolus* species. The pedicles are parallel to each other in mature individuals. The claim that pedicles are more divergent in younger individuals (Korotkevich, 1974) is doubtful and based on a deformed specimen. Upper molars have a hypoconal spur and a very small basal pillar, while the cingulum is not developed. *Palaeomeryx* fold in lower molars is very weak (Korotkevich, 1974). The premolar/molar length ratio varies between 65.5% and 70.7% with a mean value of 67.5 mm.

Genus *Pliocervus* Hilzheimer, 1922

Synonymy:

Ctenocervus Kretzoi, 1941
Ctenocerus Kretzoi, 1968

Nomenclatural acts: In 1922, Hilzheimer proposed the genus name *Pliocervus* for *Cervus matheroni* Gervais, 1852, which he believed represented an early evolutionary stage of modern deer. However, the genus definitions proposed by several authors have remained confused and contradictory. Part of the taxonomic confusion stems from the poor or misinterpreted figures provided by Gaudry (1873, 1878). Gaudry (1873: pl. XIII) published the first detailed description and figures of *Cervus matheroni*, including an antlered frontlet, two incomplete antlers, an upper tooth row, and a fragment of a lower jaw with a molarized P_4 (this specimen was not found in the collection from Mont Luberon stored in MNHN). These materials were recovered from the fossiliferous site where the original Gervais' (1852) material was discovered, and they largely influenced subsequent descriptions of the genus *Pliocervus*.

Later, Gaudry (1878) proposed an antler reconstruction of *C. matheroni* with three tines based on the earlier described incomplete specimens. Aleksejev (1915) regarded the dentition of *P. matheroni* as morphologically advanced, hypsodont, with a highly molarized P_4 and lower molars that have lost their *Paleomeryx* folds.

According to Godina et al. (1962), *Pliocervus* is characterized by well-developed cingulum in upper molars, hypsodont molars without the *Palaeomeryx* fold, and three-tined antlers with a high insertion of the first tine. Godina et al. (1962) and Korotkevich (1970) used Gaudry's (1878) questionable antler reconstruction as an illustration of the antler morphology of *Pliocervus*.

Korotkevich (1970, 1988) did not confirm the presence of cingulum in the upper molars of Pliocervus and supplemented the diagnosis with some characteristics of pedicles. These are defined as short, divergent, and somewhat compressed anteroposteriorly and are based on the cranial material of *Procapreolus* (Croitor et al., 2020). Azanza (2000) provided a similar diagnosis that defines the pedicles of *Pliocervus* as short, divergent, and inclined caudally.

Gentry (2005) noted the inadequate distinction between *Procapreolus* and *Pliocervus* and proposed that the genus should be restricted only to its type species, *Pliocervus matheroni*. The revision of some species previously ascribed to Pliocervus confirmed this viewpoint. Specifically, *Pliocervus kutchurganicus* Korotkevich, 1965 is now recognized as a junior synonym of *Procapreolus moldavicus* (Janovskaya, 1954), while *Pliocervus graecus* Azanza, 1995 is a junior synonym of *Procapreolus pentelici* (Dames, 1883) (Croitor and Stefaniak, 2009; Croitor, 2018b).

Antler remains previously described by Azanza (2000) as *Pliocervus* aff. *matheroni* from the Late Miocene of El Arguillo and Milagros (Spain) are now recognized as belonging to *Procapreolus*. The systematic position of *Pliocervus turoliensis* Azanza, 2000 from the Late Miocene of Milagros (Spain) is not clear, since it lacks the diagnostic characteristics of *Pliocervus*. *Pliocervus karabastuzicus* Abdrakhmanova, 1974 from the *Hipparion* fauna of the Karabastuz Lake area (Eastern Kazakhstan) is based on a two-tined antler with a high sat bifurcation and circular to oval beam cross-sections (Abdrakhmanova, 1974). The type antler of "*Pliocervus*" *karabastuzicus* gradually extends anteroposteriorly from the one-third of the basal segment length towards the ramification and does not show any morphological feature that could link the Karabastuz deer to *Pliocervus* from Mont Luberon.

Diagnosis: Pedicles are rather long: their posteromedial length in mature individuals moderately exceeds the pedicle diameter. The pedicles are parallel, inclined caudally, and lie on the plane of the frontal bones. The pedicles are situated close to each other: the pedicle diameter in mature individuals exceeds the distance between pedicles. Antlers are relatively large, four-tined, and lyre-shaped. The proximal part of the antler beam is cylinder-shaped. The first ramification is situated very high: the height of the ramification is 4-5 times longer than the diameter of the antler above the burr. The antler segment between the first and second tines is shorter than the distance between the burr and the first tine. The second tine is inserted on the anterior side of the beam, compressed lateromedially, and characterized by the subtriangular cross-section. The antler beam between the second tine and the distal bifurcation is slightly compressed lateromedially, with an irregular subtriangular cross-section in its distal portion. The antler surface is sculptured with longitudinal furrows and ridges, not pearled. Upper canines are large and sabre-shaped. The dentition is brachyodont. P^2 is elongated, with an additional internal enamel fold. Upper molars with large protoconal fold and small entostyle. P_4 is not molarized. Lower molars with a well-developed *Palaeomeryx* fold.

Type species: *Cervus matheroni* Gervais, 1852.

Composition: the genus is monotypic.

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

Pliocervus matheroni (Gervais, 1852)

Nomenclatural acts: The species name *Cervus matheroni* was first introduced in a report summary by Gervais (1852), based on fossil material from Mont Luberon near Cucuron. Later, Gervais (1859) provided a definition of *C. matheroni* from Cucuron (Vaucluse, southeastern France) that generally corresponded to the initial summarized report. Gaudry (1873) described and depicted additional material of the Cucuron cervid that was spelled as *C. matheronis*. Although Gaudry's (1873) work contained the first published figures of *C. matheroni*, the original material used by Gervais (1852, 1859) for the species description remained undescribed. Contrary to my earlier suggestion (Croitor, 2014), the fossil remains figured by Gaudry (1873) cannot be considered as type specimens of *C. matheronis* since Gaudry's *Cervus matheronis* is just an incorrect spelling of *C. matheroni* Gervais, 1852. According to Gaudry (1873), the original material from Cucuron is stored in the British Museum (NHML). Dawkins (1878) proposed a formal species diagnosis based on the material in the NHML, supplemented with the description and the figure of the specimen that should be regarded as a holotype. The origin and taxonomic value of the cervid material from Cucuron stored in the NHML is confirmed by Lydekker (1885), who indicated that the cervid remains in question belong to the "Bravard Collection" that was purchased by the Museum in 1852, i.e., soon after Gervais' (1852) public report at the Academy of Sciences and Letters of Montpellier.

Synonymy:

1852 *Cervus matheroni* sp. nov.: Gervais, p. 10.
1873 *Cervus* (*Axis*) *matheronis* Cervais, 1852: Gaudry: p. 65, pl. XIII, figs. 1-7.
1877 *Cervus matheroni* Gervais, 1852: Dawkins, p. 404, text-fig. 1.
1885 *Capreolus matheroni* (Cervais, 1852): Lydekker, p. 77, fig. 6 A.
1922 *Pliocervus matheroni* (Cervais, 1852): Hilzheimer, p. 743.
1970 *Pliocervus matheroni* (Gervais, 1852): Korotkevich, p. 120, fig. 18.
2014 *Pliocervus matheronis* (Gervais, 1852): Croitor, p. 125.

Holotype: the almost complete left (?) antler with pedicle BM34623 (NHML) (Dawkins 1878: fig. 1; Lydekker 1885: fig. 6 A).

Diagnosis. The body size is similar to that of modern European roe deer. The fully developed antlers are four-tined, not palmated, and relatively long (ca. 40 cm). The lower premolar series is short if compared to other Late Miocene cervids and attain ca. 66% of the molar series length.

Locus typicus: Mont Luberon (= Léberon) near Cucuron (Vaucluse, France) (Pernègre and Tassy, 2014: fig. 1).

Other sites: Aubegnas (Ardeche, France) (Torcapel, 1882).

Stratum typicum: Upper Miocene of Mont Luberon.

Description: The size of the deer is similar to that of modern roe deer; however, its antlers are relatively larger than those of *C. capreolus*. The frontal bones are narrow, with a small space between the pedicles, which is less than the transverse diameter of the pedicle. The contraction of the forehead in front of the pedicles is not expressed. The breadth of the forehead is 74 mm. The right pedicle is slightly distorted and displaced inward, which modifies its natural orientation. The pedicles are long (their length exceeds their transverse diameter), with a parallel orientation to each other, strongly inclined backwards, and situated in the plane of the frontal bones. The pedicles are compressed in the anteroposterior direction, giving them an elliptical transverse section shape. The forehead profile is straight. Each frontal bone is slightly concave in front of the pedicle. The lateral sides of the frontals are bordered with longitudinal bony ribs.

The antler beams are lyre-shaped and moderately divergent. The antlers' surface is covered with rather broad longitudinal ribs and furrows. The distal portions of the antlers are destroyed. The length of the right antler fragment is 165 mm, and the length of the left antler fragment is 255 mm. The transverse section of the antler base is circular. The basal portion of the antler beam (between the burr and the first ramification) is more or less cylinder-shaped. The lateral side of the right antler has a longitudinal depression that starts from the first tine base and runs downward. The first tine is situated very high above the burr. The first tine is compressed from the sides in its proximal portion and then becomes cylinder-shaped in its distal portion. The angle of the first ramification is 60° in the right antler and 50° in the left antler.

The second segment of the antler beam (between the first and the second ramifications) is shorter than the basal one. The transverse section of the second beam segment has an irregular rounded shape with a flattened lateral side. The second tine is situated on the anterior side of the beam, like the first tine. The basal portion of the second tine has an irregular oval shape (its measurements amount to 27.1 mm × 23.0 mm); the distal portion of the tine is acinaciform, curved and compressed from the sides (28.1 mm × 17.6 mm). The angle of the second ramification amounts to 70°. The transverse section of the antler beam above the second ramification approaches an irregular triangle shape.

There are two less robust distal portions of antlers from Cucuron that belong to the same species (Fig. A.6). The two fragments represent the second and third ramifications, with the third ramification being poorly developed in one of the fragments. However, the second fragment is better preserved and has a quite strong third ramification, although it is still significantly damaged and partially reconstructed (Fig. A.6 C, D). The distal bifurcation is formed by a stronger posterior tine (which is destroyed) and a more slender anterior tine. The third tine is gently curved inward and has a length of 92 mm. The cross-section of the antler beam is irregular, with a flattened medial side and convex lateral side. A rather sharp keel runs along the posteromedial side of the beam between the second and third ramifications. The third segment of the antler beam (between the second and third tines) is approximately 140 mm in length, and the angle of the distal ramification is 50°.

Upper teeth: The lingual wall of P^2 (second premolar) is unsplit and ungrooved (Fig. A.7 A). A small enamel fold supplements the hypocone of P^2. The lingual wall of P^4 (fourth premolar) is also unsplit and supplemented with two enamel folds: a smaller internal fold and a larger external one. Upper molars feature a well-developed protoconal fold, but the hypoconal fold (eperon, hypoconal spur) and cingulum are absent. The entostyle is weak, and the tooth enamel is wrinkled. The anterior lingual rib of the molars (parastyle) is sharp and robust, while the posterior lingual rib (metastyle) is weak. The lingual wall of the upper molars slopes significantly and forms an angle of 55° with the labial wall. Gentry (2005) reported a large left upper canine from Mont Luberon (stored in NHML), which likely belongs to *Pliocervus matheroni*.

Lower teeth: The fourth lower premolar (P_4) retains a primitive morphological condition and is not molarized (Fig. A.7 B). Its parastylid and paraconid are weakly separated, while the metaconid is extended anteroposteriorly. Lower molars are characterized by a strong ectostylid, and M_3 is supplemented with two ectostylides. Although hardly visible, the *Palaeomeryx* fold is present. The premolar series of the lower teeth is relatively long, with the premolar to molar length ratio amounting to 66.3%.

Distribution: Late Miocene of Western Europe. Morales (1984) reported the Late Miocene (MN13) of Spain a fragment of the mandible with primitive unmolarized P_4 as *Croizetoceros pyrenaicus*. Possibly, the Spanish specimen also belongs to *P. matheroni*.

Genus *Damacerus* Khomenko, 1913

Synonymy:

Cervocerus Khomenko, 1913
Cervavitus Khomenko, 1913
Procerus Simpson, 1945

Nomenclatural acts: Khomenko (1913) described three cervid genera and species based on well-preserved antlers with frontal bones from the Late Miocene of Taraclia (=Tarakliya, Moldova). These are *Cervavitus tarakliensis*, characterized by small two-tined antlers with very long pedicles; *Cervocerus novorossiae*, based an antlered frontlet with the two-tined right antler and the three-tined left antler; and *Damacerus bessarabiae*, which is based on an antlered frontlet with four-tined palmed antlers.

Aleksejev (1915) was the first to discuss Taraclia deer, providing indications with nomenclatural significance. He demonstrated that *D. bessarabiae* and *C. novorossiae* represented two different ontogenetic stages of antler development of the same species, and he applied the species name *D. bessarabiae* in his discussion. Thus, priority is given to this species name.

Zdansky (1925) regarded only two of Khomenko's genera as valid (*Cervocerus* and *Cervavitus*), while *Damacerus* was considered a junior synonym of *Cervocerus*. Dietrich (1938: p. 263) assumed that all three Taraclian genera and species represent the ontogenetic stages of the antler development of the same species and, following Zdansky (1925), gave priority to *Cervocerus*. However, *Damacerus* Khomenko, 1913 should be considered a senior synonym of *Cervavitus* and *Cervocerus* following the priority given by Aleksejev (1915).

Grubb (2000) recognized *Cervavitus* as the valid name for the genus based on the nomenclatural acts of Zdansky (1925) and Pidoplichko and Flerov (1952). However, this approach disregarded the earlier works of Aleksejev (1915) and Dietrich (1938), which have priority over all subsequent acts. Therefore, it is appropriate to retain the well-defined species *D. bessarabiae* based on a series of well-preserved fully-grown antlers.

Several species and subspecies from the Late Tertiary and Quaternary of Central Asia and China have been attributed to either *Cervavitus* or *Cervocerus*, according to various authors

(Zdansky, 1925; Teilhard de Chardin and Trassaert, 1937; Aubekerova, 1974; Dong and Hu, 1994; Dong, 2011; Wang and Zhang, 2014). However, the validity of assigning these Chinese forms to the cervid genus from the Late Miocene deer of Taraclia has been called into question by multiple researchers (Azzaroli, 1953; Czyżewska, 1968; Petronio et al., 2007; Croitor, 2021).

Moreover, there are several poorly represented or known species of *Cervavitus*, including *Cervavitus cauvieri*, described by Dong (1996) based on a fragment of antler with three tines from the Early Pliocene (MN14) of Montpellier (France). Another species, *Cervavitus sarmaticus* Kototkevich, 1970, is based on the poor proximal part of a shed antler from the Late Miocene of Kryvyi Rih (Ukraine). Therefore, a systematic revision of all these "*Cervavitus*" species is required.

In this regard, the genus *Damacerus* should be restricted to the type species until the systematic position of the above-mentioned cervid forms is clarified. It is important to note that the type species, *Damacerus bessarabiae*, is based on a series of well-preserved fully-grown antlers, which display clear diagnostic features that distinguish them from other cervid forms.

Diagnosis: Antlers are thin, lyre-shaped and characterized by the basic capreoline bauplan. The fully grown antlers became flattened in their distal part and may evolve an additional distal prong between two distal tines, so the fully-grown antlers are four-tined. The first ramification is situated high above the burr: the height of the ramification exceeds 2-3 times the antler diameter measured above the burr. The cross-section of the basal part of the antler is regularly circular. The cross-sections of the antler beam below the first ramification, the first tine, and the antler beam above the first ramification are sub-rectangular, irregularly triangular, and almost rectangular respectively. The first tine is never bifurcated. The cross-section of is. The antler surface is not pearled. The pedicles are quite long (pedicle height exceeds pedicle diameter), moderately divergent, sloped caudally from the face and lie in the plane of the frontal bones. The distance between pedicle bases in mature individuals exceeds the pedicle diameter. A more or less sharp bony ridge may connect the pedicle base with the orbit. Preorbital pits are moderately large. Nasal bones are long and reach the level of the anterior orbital edges. Upper canines are large and sabre-shaped. Upper molars are supplemented with an additional enamel protoconal fold and a spur of metaconule. P_4 usually is not molarized. Lower molars with a strong *Palaeomeryx* fold.

Type species: *Damacerus bessarabiae* Khomenko, 1913.

Composition: the genus is monotypic.

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

Damacerus bessarabiae Khomenko, 1913

Synonymy:

1913 *Cervavitus tarakliensis* gen. et sp. nov.: Khomenko, p. 108, pl. VI: 1, 2.
1913 *Cervocerus novorossiae* gen et sp. nov.: Khomenko, p. 108, pl. VI: 3-5.
1913 *Damacerus bessarabiae* gen. et sp. nov.: Khomenko, p. 109, pl. VI: 6-8.
1913 Pliocervinae subfam. nov.: Khomenko, pl. VII: 1-10.
1915 *Damacerus bessarabiae* Khomenko, 1913: Aleksejev, p. 57.
1925 *Cervocerus novorossiae* Khomenko, 1913: Zdansky, p. 12.
1938 *Cervocerus novorossiae* Khomenko, 1913: Dietrich, p. 263.
1941 *Cervocerus bessarabiae* (Khomenko, 1913): Simionescu and Dobrescu, p. 2, figs. 1, 2, pl. 1-5.
1950 *Cervavitus variabils* (Aleksejev, 1913): Flerov, p. 52.
1952 *Cervavitus variabils* (Aleksejev, 1913): Pidoplichko and Flerov, p. 1242.
1953 *Damacerus bessarabiae* Khomenko, 1913: Azzaroli, p. 9.
1962 *Cervavitus variabilis* (Aleksejev, 1913): Godina et al., p. 373, fig. 490.
1970 *Cervavitus novorossiae* (Khomenko, 1913): Korotkevich, p. 38, fig. 9.
1990 *Cervavitus novorossiae* (Khomenko, 1913): Vislobokova, p. 153.
2007 *Cervavitus novorossiae* (Khomenko, 1913): Petronio et al., p. 117, figs. 1-4.
2011 *Cervavitus novorossiae* (Khomenko, 1913): Lungu and Rzebik-Kowalska, p. 42.

Diagnosis: Body size is similar to that of modern roe deer. Antler beam above the first ramification tends to be lateromedially flattened and extends into small palmations in fully-grown specimens. The distal palmation is supplemented with a small accessory tine situated between the main branches of the second ramification and shows a trend to coalesce with the posterior branch. Fossa praeorbitalis are large and deep: the diameter of the fossa praeorbitalis in males attains ca. 68-69 % of the orbit diameter.

Syntypes: the complete antler with pedicle and a part of the frontal bone (Khomenko, 1913: pl. VI, fig. 6); the proximal part of shed antler (Khomenko, 1913: pl. VI, fig. 7); and the basal fragment of antler attached to a pedicle with a fragment of the frontal bone (Khomenko, 1913: pl. VI, fig. 7).

Locus typicus: Taraclia (Căușeni District, Moldova).

Other sites: Cimișlia, Chișla (Moldova).

Stratum typicum: the Upper Miocene of Taraclia, “Kagulsk Series” (Lungu and Rzebik-Kowalska, 2011).

Description. The specimen described here represents a medium-sized deer. Cranial and antler remains of mature individuals from Cimișlia (Moldova) stored in LPUB confirm that the main diagnostic features observed in the type specimen, which belongs to a juvenile individual, are also present in mature individuals. Pedicles are relatively long, with the pedicle length exceeding the pedicle diameter even in mature individuals with fully grown antlers. The sharp bony rib connecting the orbit rim with the pedicle base is also present in the skull of the young mature male from Cimișlia (LPUB, no number; Fig. A.8). However, these ribs are not preserved in the older individual from the same locality (LPUB, Nr. 511). Fully grown antlers bear three or four tines, with an unbranched basal tine located at a considerable distance from the burr and three distal tines terminating the palmated part of the antler (Tab. A.2). The height of the first ramification varies between 64 and 88 mm. The transverse section of the first tine is almost triangular (Simionescu and Dobrescu, 1941). The two distal tines are usually coalesced and form a distal terminal fork. The breadth of zygomatic arches is approximately 130 mm, and preorbital fossae are very large and deep. Additionally, the mandible from Taraklia Nr. 465 (LPUB) exhibits a primitive morphology of P_4, with molars supplemented with basal pillars and a weak *Palaeomeryx* fold.

The basal portion of the shed antler OF 1331 (MNHK) from the Late Miocene of Chisla (Moldova) should also be assigned to *D. bessarabiae*. This antler exhibits distinct features such as a high position of the first ramification (as shown in Table A.2), lateral compression of the antler, and a square-shaped cross-section of the antler beam.

Genus *Metadicrocerus* Schlosser, 1924

Nomenclatural acts: In 1924, Schlosser proposed the genus name *Metadicrocerus* for *Procervus variabilis* Aleksejev, 1913 from the Late Miocene of Eastern Europe to replace *Procervus* Aleksejev, 1913, which is preoccupied by *Procervus* de Blainville, 1840 (the junior synonym of *Rangifer* H. Smith, 1827) and by *Procervus* Hodgson, 1847 (the junior synonym of *Rucervus* Hodgson, 1838). Subsequently, Godina et al. (1962: p. 372) designated *Procervus variabilis* Aleksejev, 1913 as the type species of *Cervavitus*. However, under article 67.1 of the International Code of Zoological Nomenclature, *Cervavitus tarakliensis* Khomenko, 1913 is the only name-bearing type of the genus *Cervavitus*.

Procervus maeoticus Yatzko, 1932 is based on poorly preserved neurocranium with shed antlers (Korotkevich, 1970) and requires revision. Korotkevich (1976) mentions *Procapreolus* cf. *maeoticus* Korotkevich (*sic*!) from the Late Miocene of Horodne (Odesa Region, Ukraine), but it is not clear to which material the cited author is referring.

Type species: *Procervus variabilis* Aleksejev, 1913.

Emended diagnosis: Antlers maintain the initial roe-deer bauplan. The first ramification is situated rather low above the burr: the height of the ramification usually exceeds insignificantly the diameter of the antler above the burr, but often the first tine is situated very close to the burr. The first tine in fully grown antlers is often flattened, dagger-shaped, bifurcated or supplemented with an additional prong. The antler segment between the basal ramification and the distal fork is relatively long. In fully-grown antlers, the antler beam is flattened and the distal antler bifurcation extends into a broad bilobed palmation. Each palmation lobe may be terminated with two or three distal tines. The first tine and the antler beam often develop three or four longitudinal ribs that give a triangular or quadrangular shape to the antler sections. The pedicles are moderately long (the pedicle height in adult individuals moderately exceeds the pedicle diameter), compressed anteroposteriorly, divergent, and lie in the plane of the frontal bones. The frontal bones are devoid of lateral ridges connecting pedicles with orbits. Nasal bones are long and almost reach the level of the anterior margins of the orbits. The upper canines in males are moderately large (canine crown length attains ca. 20 mm). Upper premolars are supplemented with an additional inner enamel fold. The lingual wall of the upper second premolar is not cleft. Upper molars are supplemented with an additional protoconal enamel fold, a well-developed enamel spur of metaconule, and a small entostyle with a small but well-developed lingual cingulum. The lower premolar series is relatively long (premolar/molar ratio is ca. 67%). The lower fourth premolar is molarized. The lower molars have a well-developed *Palaeomeryx* fold and ectostylids.

Composition: the genus is monotypic.

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

Metadicrocerus variabilis (Aleksejev, 1913)

Nomenclatural acts: Korotkevich (1970: p. 33) reports a plesiometacarpal morphological condition in "*Cervavitus*" *variabilis*, however, I could not verify this statement. The differences in pedicle morphology and molarization of P_4 between *Cervavitus bessarabiensis* and *C. variabilis* might be estimated as taxonomical criteria at the genus level, if one applies the same taxonomical criteria as for other cervid groups (for instance, in the case of modern *Cervus* and *Dama*). Schlosser (1924) proposed the genus name *Metadicrocerus* for *Procervus variabilis* Alexejev, 1913 which seems to be an available taxonomical solution.

Synonymy:

1913 *Procervus variabilis* gen. nov. et sp. nov.: Aleksejev, p. 2, text-figs. 1-3, tabs. 1-2.

1924 *Metadicrocerus variabilis* (Aleksejev, 1915): Schlosser, p. 75.

1970 *Cervavitus variabilis* (Aleksejev, 1915): Korotkevich, p. 32, fig. 8.

1990 *Cervavitus variabilis* (Aleksejev, 1913); Vislobokova, p. 153.

2011 *Cervavitus variabilis* (Aleksejev, 1913); Lungu and Rzebik-Kowalska, p. 43.

2014 *Cervavitus variabilis* (Aleksejev, 1915); Croitor, p. 120, figs 1, 2.

Syntypes: see Aleksejev (1913).

Diagnosis: The body size is similar to that of modern fallow deer. The fully grown antlers are large and palmated. Fossa praeorbitalis is large and deep: the diameter of the fossa praeorbitalis in males attains ca. 70 % of the orbit diameter.

Locus typicus: the left flank of the Great Kuyalnik River valley near Petroverovka village (Odesa Region, Ukraine).

Stratum typicum: the Late Miocene of the Great Kuyalnik River valley near Petroverovka.

Other sites: Novoelizavetovka, Grebeniki, Nova Emetivka (Odessa Region, Ukraine), Cimişlia, Gura-Galbănă (Moldova) (Korotkevich 1976; Lungu and Rzebik-Kowalska, 2011).

Description: *Metadicrocerus variabilis* is a more advanced form of cervid with short, robust, and somewhat compressed anteroposteriorly oriented pedicles, and heavier antlers with frequent supernumerary tines. The fully grown antlers are flattened and often have additional tines in the distal part, while the basal tine may be bifurcated (Fig. 3.9). The skull (Nr. 43-1612 MNHK) from Novoelizavetovka shows somewhat depressed frontal bones between the orbits, but no clear bony ridges on the lateral sides. Instead, the frontal bones have smoothly rounded lateral ribs connecting the orbit with the pedicle base, as seen in modern large-sized cervids. The posterior edge of the nasal bones is rounded and does not reach the imaginary line connecting the anterior edges of the orbits. The orbitofrontal part of the skull is short, with the anterior edge of orbits situated above the anterior part of M^2. The preorbital pits are very deep and large, accounting for 70% of the orbit's horizontal diameter (Tab A.3). In terms of dentition morphology, *Metadicrocerus variabilis* is notable for its large sabre-like upper canines in males, molarized P_4, lower molars with the *Palaeomeryx* fold, and a rather long lower premolar series (the mean premolar/molar ratio amounts to 68%). The so-called "*Palaeomeryx* fold" of upper molars reported by Korotkevich (1970: p. 55) is an accessory enamel fold of protocone, a morphological condition known as the "bifurcated protocone".

Genus *Palaeaxis* Pohlig, 1911

Nomenclatural acts: The definition of the genus is quite vague. According to the description provided by Pohlig (1911), the antlers of *Cervus* (*Palaeaxis*) *loczyi* are three-pointed, with the high position of the first tine and the distal fork formed by the stronger anterior branch and slender posterior branch. This type of distal antler bifurcation, similar to that seen in modern roe and axis deer according to Pohlig's interpretation, is regarded as a transitional evolutionary stage from primitive cervids to the deer of the modern type. Schlosser (1924) included *C.*

(*Palaeaxis*) *loczyi* in *Capreolus* and supposed that *Procapreolus* from [Inner] Mongolia "was certainly somewhat related to *Capreolus loczyi* Kormos" (*sic*). Korotkevich (1970) included *C.* (*Palaeaxis*) *loczyi* in the genus *Procapreolus*. If one were to accept Korotkevich's (1970) proposal, then *Procapreolus* Schlosser, 1924 would become a junior synonym of *Palaeaxis* Pohlig, 1911. *Palaeaxis*, however, has been never used in systematic literature and may be considered *nomen oblitum*, while *Procapreolus* would be recognized as *nomen protectum*. It is worth noting that the collection of antler and frontal bone fragments described by Pohlig (1911) is not uniform and may represent several ontogenetic stages of antler development of a cervid form that is different from *Procapreolus*. The proximal antler fragment shown in Table VI is robust and resembles *Neomegaloceros gracilis* from the Late Miocene of Ukraine, while the frontal bone fragment with a short and robust pedicle (Pohlig, 1911: tab. VI, fig. 3) also resembles the morphology seen in *N. gracilis* (Korotkevich, 1971). Therefore, at least some of the original material of *Palaeaxis loczyi* cannot be included in *Procapreolus*.

The well-preserved three-tined antler from Polgardi described by Pohlig (1911) represents the basic and generalized antler structure of *Capreolinae* that is characteristic of *Procapreolus*, as well as *Eocoileus*, *Capreolus*, and *Ozotoceros*. Given the relatively conservative evolution of antlers in Capreolinae, it is difficult to assume the synonymy of *Procapreolus* and *Palaeaxis*. Therefore, a thorough revision of the original material from Polgardi is necessary.

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

Type locality: Polgardi (Fejer County), Hungary; Pannonian sandstone quarries near the village (Pohlig, 1911).

Composition: the genus is monotypic.

Distribution: the Late Miocene, Central Europe.

Genus *Capreolus* Frisch, 1775

Diagnosis: Antlers are three-pointed, with a high position of the first tine and a relatively short distance between the first and second ramifications. Antler burr is strongly developed. The antler segment between the burr and first ramification is covered with pearling and irregular tubercles. Pedicles are short, with parallel orientation and a short distance between them that roughly equals the diameter of the pedicle. P_4 is highly molarized. Upper canines are absent. Protoconal folds in upper molars are missing. Nasal bones are extended behind the line connecting the anterior edges of orbits. The posterior aperture of the nares is not divided completely by the vertical plate of the vomer.

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

Composition: *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.

Description. This is a genus of telemetacarpal deer, belonging to the subfamily Capreolinae. However, unlike the majority of its counterparts, the nasal cavity of *Capreolus* (at the posterior aperture of nares) is not divided completely by the vertical plate of vomer. Instead, *Capreolus* shares this characteristic with other Old World telemetacarpal deer, such as *Alces* and *Hydropotes* (Brooke, 1878). Although Flerov (1952) regards the roe deer *C. capreolus* as a primitive cervid that maintained some muntiacine traits, the cranial and dental morphology of *Capreolus* is very advanced. The pedicles are rather short and set in a more vertical position when compared to *Procapreolus*, with a short space between them. The nasal bones are long and extended behind the line connecting the anterior edges of the orbits. The preorbital fossae are small, much smaller than in *Procapreolus*. The upper canines are lost, similar to *Alces*, thus representing one of the rare exceptions among modern Capreolinae that typically maintain their upper canines throughout their lives. The protoconal fold in upper molars is lost, and the *Palaeomeryx* fold is never present in modern species. However, it is recorded in the earliest known species *C. constantini* from the Pliocene (MN16) of Udunga, Trans-Baikal Area (Vislobokova et al., 1995). P_4 is highly molarized, and the premolar/molar ratio varies between 69.6% and 74.6%, indicating a generally longer premolar series than in *Procapreolus* (Vislobokova and Kalmykov, 1994). The antlers maintain the three-pointed bauplan, as seen in *Procapreolus*. However, roe deer antlers are usually distinguished by the stronger development of burr and the specific pearling that covers the proximal part of the antler beam, which differs from *Procapreolus*.

Capreolus cusanoides Kahlke, 2001

Diagnosis: body size is similar to modern European roe deer. Antlers are devoid of tubercles, three-pointed, with compressed laterally distal portions. The lower premolar series is very long (ca. 90% of the molar series length). Lower molars are devoid of the *Palaeomeryx* fold.

Type locality: Untermassfeld, Germany.

Stratum typicum: Lower Pleistocene, Epifillafranchian, ca. 1.02 Ma.

Description and comments. According to Kahlke (2001), *Capreolus cusanoides* represents the earliest roe deer species known in western Eurasia. This deer is characterized as small-sized, weighing approximately 38 kg, which is comparable in body size to modern European roe deer. Kahlke (2001) observed that the antlers of the roe deer from Untermassfeld display significant similarities to those of *Procapreolus cusanus*, while the dentition morphology of *C. cusanoides* is akin to that of modern roe deer. The only complete mandible (IQW 1993/24 360) discovered from Untermassfeld displays an unusually long series of premolars, with a premolar/molar ratio of 91.1%. This feature brings the roe deer from Untermassfeld closer to the most primitive Late Miocene *Procapreolus* forms, such as *P. ucrainicus*, which also had a relatively long premolar series. However, the premolar series of *Procapreolus cusanus* from Perrier (France) is relatively shorter, and it is challenging to give an evolutionary and morpho-functional interpretation for the exceptional length of the premolar series in roe deer from Untermassfeld based on a single available specimen. Pedicles of *C. cusanoides* are described as short and robust, indicating advanced evolutionary specialization. Notably, the antler morphology of *C. cusanoides* is distinct from the typical *Capreolus* antler shape, since the presence of large tubercles in the proximal part of antlers is an important diagnostic feature of the genus (Flerov, 1952; Lister et al., 1998). The oldest Pliocene roe deer species, *Capreolus constantini*, already displays well-developed antler tubercles (Vislobokova et al., 1995). Thus, *C. cusanoides* appears to be a specialized capreoline that does not conform to the evolutionary trend within the genus *Capreolus*. Nevertheless, due to the scarcity of available remains, a definitive conclusion regarding the systematic position of this species is not yet possible.

Capreolus suessenbornensis Kahlke, 1956

Synonymy:

1953 *Capreolus capreolus* (Linnaeus): Azzaroli, p. 32.

Diagnosis (Kahlke, 1969): body size is larger than in modern European roe deer. Three-pointed antlers are characterized by strong spike-like tubercles and a flattened beam portion between ramifications. Mandibles are relatively robust: mandible thickness below M_1 attains more than half of mandible height at the same point.

Locus typicus: Suessenborn, Germany.

Stratum typicum: Middle Pleistocene, ca. 600 kyr BP.

Distribution: the Middle Pleistocene of Western and Central Europe (Lister et al. 1998; Stefaniak, 2015). This species is conspicuously absent from the paleontological record of Eastern Europe (Alekseeva, 1977).

Description. *Capreolus suessenbornensis* is a larger form of roe deer, with a body mass that could reach 40-45 kg. A flattened antler beam is the main morphological feature distinguishing this species from modern roe deer. Lister et al. (1998) consider this character to be indicative of a subspecific level. The lower part of the antler beam may coincide with the axis of the pedicle, as observed in the specimen M/K 4.7.66 (SMNH) from Mosbach, or deviate sideward immediately from the burr, forming an angle of 65-70°, as seen in specimens 32860/9 and 32860/5 (SMNH) from the same site.

The mandibular fragment 32860/3 (SMNH) from Mosbach is relatively robust, with a height of 21.1 mm and 23.2 mm below M_1 and M_2, respectively, and a thickness of 11.9 mm and 12.3 mm below M_1 and M_2, respectively. Although the measurements of the mandible from Mosbach are similar to those of modern *C. capreolus*, the body of the mandible is more robust. Specifically, the ratio between mandible thickness to mandible height below M_1 is 56.4% for the specimen in question, whereas in modern roe deer, this index ranges from 48.3% to 49.8% (n=3, Uch-Bash, Iron Age, Crimea). Lower molars (M_2 and M_3) of the right mandibular fragment 32860/10 (SMNH) from Mosbach do not show any trace of the *Palaeomeryx* fold.

Capreolus capreolus (Linnaeus, 1758)

The modern European roe deer exhibits a set of advanced cranial characteristics, such as the loss of contact between nasal and premaxillary bones in most cases, a V-shaped nasofrontal suture due to nasal bones wedged between frontals, and a relatively shorter braincase compared to Asian *C. pygargus*. The evolutionary significance and degree of specialization of specific European roe deer traits, such as the shrunken and uninflated auditory bullae that distinguish it from *C. pygargus*, is difficult to estimate (Flerov, 1952; Lister et al., 1998).

Many authors, including Czyżewska (1968), Korotkevich (1970), Vislobokova (1990), Vislobokova and Kalmykov (1994), Grubb (2000), Kahlke (2001), and Di Stefano and Petronio (2002), accept the close phylogenetic and systematic relationship between the modern *Capreolus* and its Mio-Pliocene forerunner, *Procapreolus*. This is based on the fact that *Capreolus* and *Procapreolus* share the basic antler bauplan characteristic of most of Capreolinae. This basic capreoline antler construction, with a high position of the anterior tine and a distal fork with a stronger anterior tine, can also be observed in modern *Ozotoceros* and *Alces*, as well as in the extinct *Eocoileus*. However, our knowledge of cranial morphology for most fossil forms is insufficient to confirm or reject the hypothesis of a direct phyletic relationship between *Capreolus* and *Procapreolus*.

Western forms of *Procapreolus* likely represent an extinct side lineage without living descendants. The best-known *Procapreolus moldavicus* is a primitive form with a plesiomorphic mixture of muntiacine, odocoileine, and roe deer cranial and dental characters. Some of its characteristics, such as broad frontals and divergent pedicles, rule out the direct phyletic relationship between *P. moldavicus* and *Capreolus*. While the parallel orientation of closely set pedicles in *C. capreolus* resembles the archaic capreoline genus *Pliocervus*, the latter is characterized by specialized four-pointed antlers with an irregular section of the beam. Thus, we are dealing with a broad and poorly known phylogenetic radiation of the capreolines, characterized by mosaic combinations of shared characters that exclude the possibility of direct phyletic relationships between them.

Genus *Neomegaloceros* Korotkevich, 1971

Diagnosis: Pedicles are rather short, robust, and somewhat compressed anteroposteriorly. Antlers are large and robust, with a very high position of the first tine, a posterior tine and distal palmation terminated with several crown tines.

Type species: *Neomegaloceros gracilis* Korotkevich, 1971

Composition: the genus is monotypic.

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

Neomegaloceros gracilis Korotkevich, 1971

Diagnosis: The body size is an intermediary between roe deer and fallow deer. The first tine is situated very high above the burr, unbranched, with a triangular cross-section. The antler beam is flattened and above the first bifurcation and extends into a distal palmation, which is terminated by several distal tines and bears a small posterior tine.

Holotype: Left antler with pedicle Nr. 3754 stored in the Paleontological Museum of the Odessa State University. A cast of this specimen is stored in MNHK.

Locus typicus: Ananiev, Odesa District, Ukraine.

Stratum typicum: Late Miocene, Maeotian, MN 12.

Description. The basal segment of the antler has a nearly circular transversal section, with the first tine located high above the burr (Tab. A.2) and its distal part having a triangular cross-section. The first tine is at least 120 mm long, and the antler beam becomes compressed from the sides below the first ramification. The median side of the antler is flat, while the lateral side is convex. The posterior tine is significantly compressed from the sides and situated 213.6 mm from the burr. The preserved part of the distal palmation is robust and appears to terminate with two lobes and up to five tines, according to Korotkevich (1971). The antler beam above the burr has a lateromedial diameter of 30.7 mm and an anteroposterior diameter of 33.5 mm. Korotkevich (1971) reports that the total length of the antler can reach 340 mm. The pedicle is short, robust, and anteroposteriorly compressed (L, 20.0 mm; DAP, 29.7 mm; DLM, 31.8 mm) and shows some resemblance to *Metadicrocerus variabilis*. However, the present study measurements do not match the lateromedial compression of the pedicle reported by Korotkevich (1971).

It is possible that some of the material from the Late Miocene of Polgardi (Hungary) described by Pohlig (1911) as *Cervus* (*Palaeaxis*) *loczyi* actually belongs to *N. gracilis* or a closely related cervid species. The robust fragment of a shed antler and the frontal bone fragment with a massive pedicle illustrated by Pohlig (1911) on Tab. VI suggest this possibility.

Unlike *Damacerus bessarabiae*, *N. gracilis* is characterized by short anteroposteriorly compressed pedicles. *N. gracilis* also differs from *N. variabilis* in having a high position of the first ramification and a thin, unbranched first tine. Korotkevich (1971) considered *N. gracilis* a primitive ancestor of giant deer due to the development of the distal antler palmation and the presence of a "posterior tine" that is comparable to the posterior tine in giant deer. The first ramification, according to Korotkevich (1970), is homologous to the middle tine in *Praemegaceros verticornis* and *Megaloceros giganteus*.

Genus *Cervodama* Pidoplichko and Flerov, 1952

Cervodama pontoborealis Pidoplichko and Flerov, 1952

Synonymy:

1952 *Cervus* (*Cervodama*) *pontoborealis* sp. nov.: Pidoplichko and Flerov, p. 1239, fig. 1.
1990 *Cervodama pontoborealis* (Pidoplichko and Flerov): Vislobokova, p. 158.
2006 *Alces alces* (Linnaeus): Croitor, p. 104-105, fig. 18.

Nomenclatural acts. The species was described by Pidoplichko and Flerov (1952) based on a well-preserved left shed antler found in the Pliocene deposits of Mariupol (Ukraine). Pidoplichko and Flerov (1952) noted that the palmated part of the antler resembled that of modern *Dama mesopotamica*. However, Korotkevich (1970) and Vislobokova (1990) considered *Cervodama pontoborealis* to be a deer with an uncertain taxonomic position, as it also exhibited similarities with modern elk. Croitor (2006b) suggested that *Cervus* (*Cervodama*) *pontoborealis* be included in the synonymy of modern *Alces alces*. Nevertheless, the specific characteristics of the antler morphology and the uncontested Pliocene age of the antler from Mariupol indicate that this deer represents a distinct form that belongs to the early evolutionary radiation of the subfamily Capreolinae (Croitor, 2021).

Diagnosis: A small deer similar in size to modern fallow deer. The antler beam is very short (ca 4 cm from the burr). The distal palmation is broad, fam-shaped and terminated by several tines (up to seven). The two tines that spring off from the posterior part of the palmation are stronger and longer than other antler tines.

Holotype: the almost complete shed left antler Nr. 434 stored in the Museum of Local History of Mariupol.

Locus typicus: Mariupol, Kalmius River mouth, Ukraine.

Stratum typicum: the Pliocene sands near the Kalmius River mouth (Late Miocene – Pliocene according to Vislobokova, 1990).

Description. The antler found in Mariupol is characterized by a well-developed burr (D – 56 mm) and a relatively thin main beam that reaches a maximum diameter of 35 mm. The beam forms a broad palmation 4 cm from the burr, which is fan-shaped with six radial tines, rather than forming a clear main axis like antlers of a cervid similar to modern *Dama mesopotamica*. The proximal part of the antler is a short basal segment, similar to modern *Alces alces*. The palmation is well-developed but narrower than in modern elks, with an angle between the anterior and posterior edges of 105°, compared to 180° in modern *A. alces*. The antler has three long and robust tines: the anterior tine, possibly bifurcated, represents the first capreoline ramification, while the two strongest posterior tines correspond to the distal bifurcation. Four smaller tines are present between the first ramification and the distal fork, resembling the way modern *A. alces* develops additional prongs. The elk from Udunga (Baikal Area, Russia) has typical modern *Alces* sideward orientation of pedicles, and its antler base diameters (40.3×43.0 mm, 59.3×65.0 mm: Vislobokova et al., 1995) exceed those of the deer from Mariupol. Notably, the antlers of *Cervodama* resemble those of *Antifer ultra* from the Pleistocene of South America, which represents an example of convergent evolution.

Distribution: Late Miocene - Pliocene, Southeastern Europe.

Genus *Croizetoceros* Heintz 1970

Nomenclatural acts. Heintz (1970) assumed the plesiometacarpal morphological condition for *Croizetoceros*, although this assumption remains unconfirmed. Pfeiffer-Deml (2016) placed *Croizetoceros* in the subfamily Capreolinae and this viewpoint is followed in the present study.

Diagnosis: see Heintz (1970).

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

Composition: *Croizetoceros ramosus* (Croizet and Jobert, 1828) (Late Pliocene, Western Europe); *Croizetoceros proramosus* Dong, 1996 (Early Pliocene, France).

Croizetoceros ramosus (Croizet and Jobert, 1828)

Diagnosis: see Heintz (1970).

Description. This is a relatively small deer with large, intricate antlers and advanced dentition morphology (Heintz, 1970). Its estimated body mass is around 50-55 kg. The antler shape of *C. ramosus* is distinctive and does not show a clear affinity with any known group of cervids. The basal tine is positioned high above the burr, followed by a series of crown tines inserted on the anterior side of the beam, with more or less equal distances between them. A fully grown antler may have 6-8 tines (Heintz, 1970). The cheek teeth morphology exhibits the unusual Pliocene Cervinae combination of characters: P_4 is always molarized, the *Palaeomeryx* fold can be vestigial or absent, and the small protoconal fold and hypoconal enamel spur are present in upper molars. The cranial remains of *C. ramosus* are rather sparse and do not provide systematically significant characteristics. The antlered skullcap 1923-4 from Sénèze (MNHN) is one of the most complete specimens (Fig. A.10). The frontal bones are flattened, and the forehead behind the orbits is sharply narrowed (the breadth at posterior edges of orbits is 118.5 mm; the frontal breadth is 85.3 mm; the breadth behind pedicles is 71.6 mm). The pedicles are rather short (their length does not exceed transversal diameter), divergent, and somewhat inclined caudally; the parietal bones are flat, and the braincase seems to be relatively long. According to Heintz (1970), the preorbital pits are large and deep, and the ethmoidal openings are large. Heintz (1970) also cites J. Viret's statement regarding the presence of upper canines. The relative length of the lower premolars is similar to *Pliocervus* (66%).

There is no conclusive evidence of the presence of *C. ramosus* in Central and Eastern Europe, except for some sparse Early Villafranchian remains from Poland and Slovakia (Czyżewska, 1972; Stefaniak, 1995, 2015; Sabol, 2003). *C. ramosus* was abundant in the Villafranchian of Western and Mediterranean Europe (Heintz, 1970; Kostopoulos and Athanassiou, 2005) and became extinct shortly after the *Pachycrocuta*/"wolf" event. It appears that *C. ramosus* was an ecological counterpart of *Procapreolus moldavicus*, which, in turn, is not known in Western Europe but is prevalent in Central and Southeastern Europe. There are no remains of *Croizetoceros* or a similar cervid found in Asia, indicating that *Croizetoceros* is an endemic European genus. Dong (1996) described *Croizetoceros proramosus* from the Early Pliocene of France. The species is based on dental remains only, and we know nothing about its antlers and other parts of the skeleton. This species is already characterized by the advanced molarization that distinguishes it from the deer of the subfamily Cervinae of that epoch

Distribution: Pliocene – Early Pleistocene (MN16-18), Western Europe.

Genus *Alces* Gray, 1821

Synonymy:

Alce Cuvier et al., 1827
Praealces Portis, 1920

Libralces Azzaroli, 1952
Latifrons Nikolsky, 2010

Nomenclatural acts: The Latin zoological name for elks is *alce*, with the plural form *alces*, which appears in pre-Linnean publications (Gessner, 1551: p. 1; Aldrovandi, 1621: p. 866; Jonston, 1652: p. 96; Ray, 1693: p. 86). In 1821, Gray established the genus *Alces* within the composition of Cervidae, with the type species *Cervus Alces* Linneus. Later, Cuvier et al. (1827) described the subgenus *Cervus* (*Alce*) with a diagnosis and synonymy. The authorship is attributed to H. Smith (see Lydekker, 1913), and *Alce* H. Smith falls in the synonymy of *Alces* Gray (Lydekker, 1913).

Azzaroli (1952) established a new genus, *Libralces*, with the type species *Libralces gallicus* from the Villafranchian fauna of Sénèze. It is distinguished by its primitive cranial and dental characters, such as the long nasal bones articulated with premaxillary bones and the *Palaeomeryx* fold in the lower molars. Later, Azzaroli (1985) proposed regarding *Libralces* as a subgenus of the North American genus *Cervalces* Scott, 1885, which is characterized by a similar shape of the muzzle. Vislobokova (1986, 1990) and Boeskorov (2001) recognize three valid genera of elks: *Libralces* Azzaroli 1952 with the type species *Libralces gallicus* Azzaroli, 1952; *Cervalces* Scott, 1885 with the type species *Cervalces scotti* (Lydekker, 1898), and the modern genus *Alces*.

Breda (2001) and Stefaniak (2007) included all fossil elks in the genus *Cervalces*. This taxonomical solution is accepted by Nikolsky (2010), who divides *Cervalces* into three subgenera: *Libralces*, *Cervalces*, and *Latifrons*. According to Nikolsky (2010), *Cervus latifrons* Johnson, 1874 is the type species of the subgenus *Cervalces*. On the other hand, Kahlke (1969), Heintz and Poplin (1980), Lister (1987), and Brugal and Croitor (2007) included all elk species in *Alces*. In defense of the latter point of view, it can be pointed out that all recorded characters distinguishing fossil and modern forms of elks concern only exosomatic organs (muzzle shape and details of antler morphology) and body size, which are used to distinguish species within a genus.

Diagnosis: The nasal cavity (at the posterior aperture of the nares) is not divided completely by the vertical plate of the vomer. The pedicles are directed sideward, and the antler beams are horizontally oriented sideward and greatly vary in length. The general bauplan of unpalmated elk antlers maintains the basic antler type of Capreolinae. The general antler construction is characterized by the development of main 3-5 tines: the first (basal) tine is directed toward the anterior, often double or bifurcated; the antler beam is bent toward the posterior in the area of the first bifurcation and the simplest case is terminated by a fork, but supernumerary tines are often present on the anterior side of the beam. Antlers often develop distal palmations. Lower premolars P_3 and P_4 are highly molarized: P_4 is functionally molariform, while P_3 represents the advanced degree of molarization with complete fusion of metaconid and paraconid. The lower molar series is relatively long: the premolar to molar series length ratio varies between 67.0 and 74.3%. The *Palaeomeryx* fold is present in primitive forms.

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.

Comments. The elks are telemetacarpal deer. However, unlike American telemetacarpal cervids, their nasal cavity at the posterior aperture of nares is not completely divided by the vertical plate of the vomer. This specific characteristic brings *Alces closer* to *Capreolus* and *Hydropotes* and distinguishes them from their American counterparts (Brooke, 1878). In *Alces*, evolutionary modifications of antler morphology concern only the number of supernumerary points, which typically merge in a terminal antler palmation, and the length of the basal segment of the antler, which is located between the burr and the first/basal ramification.

Alces gallicus (Azzaroli, 1952)

Synonymy:

1952 *Libralces gallicus* sp. nov.: Azzaroli, p. 134, fig. 1.
1953 *Libralces minor* ssp. nov.: Azzaroli, p. 18, fig. 4.
1985 *Cervalces* (*Libralces*) *gallicus* Azzaroli, 1952: Azzaroli, p. 179.
2010 *Cervalces* (*Libralces*) *minor* (Azzaroli, 1952): Nikolsky, p. 13.
2010 *Cervalces* (*Libralces*) *gallicus* (Azzaroli, 1952): Nikolsky, p. 13.

Nomenclatural acts: In 1952, Azzaroli designated the heavily damaged and partially reconstructed articulated skeleton Nr. 96134 (PMUL) as the holotype of *Libralces gallicus*. However, Breda (2001) expressed doubts that the antlered skull and postcranial mounted skeleton exposed in the PMUL belong to the same individual and excluded the mounted postcranial bones from the holotype. According to Breda (2001), the better-preserved articulated bones of a somewhat larger individual from the same locality, which Azzaroli had chosen as the cotype, belong to the same individual together with the antlered skull. Therefore, Breda proposed that those postcranial bones should be considered as parts of the holotype of *Libralces gallicus*.

Diagnosis: The nasal bones are articulated with premaxillary bones. The braincase is relatively short: the distance between bregma and opisthocranion is shorter than the breadth of the neurocranium behind pedicles. Upper molars are characterized by the presence of a large protoconal fold; the hypoconal spur is absent. A weak *Palaeomeryx* fold may occasionally be present on lower molars. P_3 is not fully molarized: its metaconid and paraconid are not fused. Beams of full-size antlers are longer than the condylobasal length of the skull. Antlers are terminated with fan-shaped palmations.

Holotype: partially reconstructed articulated skeleton Nr. 96134 (PMUL).

Locus typicus: Sénèze, France.

Stratum typicum: the Early Pleistocene lacustrine "maar" deposit dated back to 2.0-1.6 Ma (Breda, 2001).

Description. The skull of *A. gallicus* is characterized by the specific sideward direction of the pedicles, a feature also seen in modern elks, and is distinguished from modern *A. alces* by its low and broad braincase (Azzaroli, 1952; Breda, 2001) and the obtuse angle between occipital and parietal surfaces. The nasal bones are rather long and articulated with the praemaxillae. The orbital part of the type skull is destroyed and has been reconstructed with plaster, making it impossible to measure the condylobasal length accurately. The distance between bregma and opisthocranion is shorter than the breadth of the neurocranium behind pedicles in the skull M6101 from East Runton (Tab. A.4). The breadth of the braincase is 51.2% of the breadth of the frontals. The angle between the horizontal ramus of the mandible and its ascending part is 110° (Azzaroli, 1953: p. 28, fig. 10A). Based on the holotype skull from Sénèze and the skull fragment from East Runton (M6101, NHML), the estimated body mass is approximately 400 kg.

One of the most striking morphological features of *A. gallicus* is the extremely long basal segment of the antler between the burr and the distal palmation. The antler beam is set along the pedicle axis, and the position of the burr is oblique to the beam axis (Breda, 2001). The antler beams of the type specimen are gently curved and terminate with fan-shaped palmations supplemented with cone-shaped tines, with only two terminal tines preserved on the left antler. The antler beam is much longer than the palmated part of the antler. The total span of antlers could reach up to 2.20 m (Azzaroli, 1952).

The upper molars, including at least M^3, are characterized by the presence of a large protoconal fold, while the hypoconal spur is absent. Large entostyles and weak lingual cingula supplement the upper molars (Breda, 2001). The lower molars have strong ectostylids. Azzaroli (1952) initially claimed that the lower molars of the mandible from Weybourne Crag, ascribed to *A. gallicus*, had a weak *Palaeomeryx* fold. However, Heintz and Poplin (1980) and Breda (2001) have since disproven this claim, as it is not visible in the holotype from Sénèze. Nonetheless, Azzaroli (1952) was clearly referring to the specimen from Weybourne Crag, not to the type specimen from Sénèze. My study confirms that the weak *Palaeomeryx* fold is present in M_1 and

M_2 of specimen M6227, the holotype of *Libralces minor*. Nikolsky and Titov (2002) also reported the presence of a weak *Palaeomeryx* fold in the lower molars of *A. gallicus* from Liventsovka, Russia. Therefore, the occasional presence of a vestigial *Palaeomeryx* fold should be considered a specific character of *A. gallicus*. Azzaroli (1952, 1953) suggested the possible presence of upper canines in *A. gallicus*, but this presumption was not confirmed by other authors (Heintz and Poplin, 1980; Breda, 2001).

Unlike geologically younger elks, P_3 in *A. gallicus* has not fully molarized: the metaconid and the paraconid in P_3 of the specimens M6227 and M6206 from the Cromer Forest Bed formation are not fused (Azzaroli, 1953: fig. 4) and this feature represents a distinguishing primitive character. It is difficult to make a reliable comparison with the holotype from Sénèze, which is characterized by a complete fusion between the metaconid and the paraconid (Azzaroli, 1952: fig. 2a), but the wearing stage of its dentition is much more advanced. It is important to mention that the similarly unmolarized P_3 with the open anterior valley is also characteristic of Cervalces scotti Lydekker from the Holocene of North America (Hibbard, 1940: pl. II, fig. 1).

Distribution. Remains of *A. gallicus* are known from France, England, Romania, the Azov Area of Russia, and Tajikistan (Azzaroli, 1952, 1953; Heintz and Poplin, 1980; Vislobokova, 1986; Boeskorov, 2001; Nikolsky and Titov, 2002; Breda and Marchetti, 2005; Radulescu, 2005). However, the fragment of antler palmation from Dmanisi previously reported as *A. gallicus* (Krijgsman et al., 2019) has been re-determined as belonging to *Sinomegaceros insolitus*.

Alces carnutorum (Laugel, 1862)

Synonymy:

1862 *Megaceros carnutorum* sp. nov. (partim): Laugel, p. 712, fig. 1.
1874 *Cervus carnutorum* (Laugel, 1862): Johnson, p. 3.
1980 *Alces carnutorum* (Laugel, 1862): Heintz and Poplin, p. 107, figs. 1, 2.
2007 *Cervalces carnutorum* (Laugel, 1862): Stefamiak, p. 75, tabs. I-III; figs. 1-1F, 2-9.
2010 *Cervalces* (*Libralces*) *carnutorum* (Laugel, 1862): Nikolsky, p. 13.

Nomenclatural acts: Laugel's (1862) original description of *Megaceros carnutorum* was based on cervid remains from Saint-Prest (France) that included remains of two large-sized deer: an elk and a plesiometacarpal deer. The first review of the species was conducted by Heintz and Poplin (1980), who chose the fragment of the left maxilla SPR-70 (MNHN) as a lectotype. Given the fragmentary and incomplete nature of the fossil material from Saint-Prest, Heintz and Poplin (1980) did not rule out the possibility of *A. carnutorum* being a subspecies or synonym of *A. gallicus* or *A. latifrons*.

Diagnosis: the body size is intermediate between *A. gallicus* and *A. latifrons*. Protocone in upper molars is bifurcated. The enamel folds of the bifurcated protocone tend to get in touch at their ends and isolate an enamel fold. The entostyles in the upper molars are well-developed.

Lectotype: fragment of the left maxilla SPR-70 (MNHN) with M^1 and M^2.

Locus typicus: Saint-Prest, France.

Stratum typicum: the final Early Pleistocene

Description. Molars of *A. carnutorum* have low crowns with a strongly sloped lingual wall, resulting in an angle of 50° between the labial and lingual walls of the molars. The posterior wing of the protocone is supplemented by a protoconal fold, and both the protoconal fold and the posterior wing of the protocone in M^1 and M^2 tend to close the small enamel isle between them. While the hypoconal spur is not present in M^1, it is well-developed and folded in M^2. The entostyle is also well-developed, particularly in M^2. The length of the M^1 crown measures 27.1 mm, and the maximum breadth at the crown base is 28.3 mm; the corresponding measurements for M^2 are 30.3 mm and 29.0 mm.

Stefaniak (2007) reported on the poor remains of *A. carnutorum* recovered from the Biharian deposits of Zabia Cave. These remains comprised of isolated teeth, fragments of mandible, and limb bones. The isolated incisives (I_1 and I_2) exhibited symmetric chisel-like crowns, which are also characteristic of modern *A. alces*. Additionally, the isolated P_3 (as shown in Stefaniak, 2007: fig. 1B) displayed incomplete molarization, similar to that observed in *A. gallicus* from the Cromer Forest-Bed formation. Further examination of the upper molars from Zabia Cave (L M1 = 25.3-25.9 mm, n=2; L M2 = 27.6-28.8 mm, n=2) revealed that they were slightly smaller than the lectotype from Saint-Prest. The fragment of the mandible from Zabia Cave is characterized by a more acute angle (96°) between the mandibular body and its ascending part compared to the modern elk (110°) (Stefaniak, 2007). This acute angle between the horizontal and ascending parts of the mandible is associated with a relatively shorter orbitofrontal part of the skull in the elk from Zabia Cave. Notably, the presence of the *Paleomeryx* fold was not reported (Stefaniak, 2007).

. The pedicle of *A. carnutorum* from Saint-Prest is robust and directed sideways, with a somewhat compressed dorsoventral diameter similar to that of *A. gallicus*, measuring 55 mm in the dorsoventral direction and 60 mm in the anteroposterior direction (Heintz and Poplin, 1980). The postorbital (=frontal) breadth, based on the left frontal bone which was badly preserved, measured 210 mm, slightly below the measurements of the elk sample from Mosbach (220-230 mm according to Heintz and Poplin, 1980) and *A. gallicus* from East Runton..

Distribution. The species is reported from France, Germany, Northern Italy, Romania, Moldova and Poland (Heintz and Poplin, 1980; Kahlke, 1997; Radulescu, 2005; Stefaniak, 2007).

Alces sp. from Mosbach

Description. The discovery of elk remains from Mosbach (Germany) exposes the inadequacy of the current taxonomic model for fossil elks and highlights the insufficient knowledge of their morphology and intraspecific variation. Despite the abundance of elk remains from Mosbach, they cannot be confidently assigned to any recognized species due to the unknown stratigraphic provenance of the material. Mosbach contains two distinct levels; one is comparable in age to other European sites with *A. latifrons*, and the other to European sites with *A. carnutorum* (Breda and Marchetti, 2005). The inability to assign the Mosbach material to a specific species highlights the need for a more comprehensive understanding of the morphological distinctions between the aforementioned species. Notably, the left hemimandible 3286/5 (SMNH) displays a weak trace of the *Palaeomeryx* fold in M_1 and M_2 (Fig. A.11). M_3 also exhibits an enamel fold that bears similarity to the *Palaeomeryx* fold. P_4 is molariform, and P_3 is molarized, with its metaconid and paraconid fused and closing the anterior valley from the lingual side.

The advanced molarization of P_3 distinguishes the elk from Mosbach from samples described as *A. gallicus* and *A. carnutorum*. The angle between the body of the lower mandible and its ascending part is 130°, which is significantly larger than the value reported for *A. carnutorum* from Zabia Cave. The fragment of the right hemimandible 32861/33 (SMNH) from *Mosbach* with M_2 also shows a clear rudiment of the *Palaeomeryx* fold.

The maxilla Nr. 32861/8 with M^2 and M^3 (L M^2 = 33.0 mm; D M^2 = 31.0 mm; L. M^3 = 31.1 mm; D M^3 = 30.0 mm) is somewhat larger than the lectotype of *A. carnutorum*. The styles of both molars are strong and protruding, and the protoconal fold is present, which, together with the posterior wing of M^2, isolates a small enamel isle as in *A. carnutorum*. The spur of the hypocone is absent in M^2 and well-developed in M^3. The entostylid is vestigial in M^2 and better developed in M^3, but much still smaller compared to the lectotype of *A. carnutorum*.

The elk from Mosbach is characterized by advanced features such as the absent lingual cingulum and reduced entostylids, molarized P_3, larger angle between the mandibular body and the ascending ramus of the mandible, combined with comparatively small size and a vestigial *Palaeomeryx* fold.

Alces latifrons (Johnson, 1874)

Synonymy:

1874 *Cervus latifrons* sp. nov.: Johnson, p. 2, pl. 1.

1920 *Cervus* (*Praealces*) *latifrons* Dawkins et Johnson: Portis, p. 137.

1953 *Libralces reynoldsi* sp. nov.: Azzaroli, p. 19, figs. 5b, 6-8, 9c.

1953 *Libralces latifrons* (Johnson, 1874): Azzaroli, p. 27, figs. 10b, c, 11.

1962 *Alces palmatus* Ham. Smith: Macarovici, p. 66, pls. 1, 2.

2010 *Cervalces (Latifrons) latifrons* (Johnson, 1874): Nikolsky, p. 13.

Nomenclatural acts: The original description of *Cervus latifrons* provides a diagnostic description along with measurements and figures (Johnson, 1874). Azzaroli (1953) proposed a new species name, *Libralces reynoldsi*, for an extremely large form of elk from Mundesley and the Cromer Forest Bed Formation. According to Azzaroli (1953), *Libralces reynoldsi* is a large-sized descendant of *Libralces gallicus*. Azzaroli (1953) included *Cervus latifrons* in the genus *Libralces*, but considered this species as poorly defined, with an intermediate body size between gallicus and reynoldsi.

Diagnosis: the braincase is relatively long: the distance between bregma and opisthocranion measured in the skull from Mundesley is significantly longer than the braincase breadth measured behind pedicles. The protoconal fold in the upper molars is weak. The metaconid and the paraconid of P^3 are fused. Antler beams are shorter than condylobasal length. The palmed part of the antler is larger than the antler beam.

Syntypes: A left antler with a part of palmation and anterior tine attached to a part of the frontal bone and a nasal portion of the left antler attached to the frontal bone, Norwich Museum, both figured by Johnson (1874).

Locus typicus: Hasbro (= Happisburgh: Azzaroli, 1953), Forest-Bed, Norfolk.

Stratum typicum: Middle Pleistocene.

Description. This is one of the largest fossil cervid species in the Western Palearctic, with a body mass estimated at 870 kg based on the skull M6553 from Mundesley, NHML. The skull M6553 is characterized by its elongated neurocranium in comparison to *A. gallicus*, with the distance between bregma and opisthocranion significantly longer than the braincase breadth measured behind pedicles (Table A.4). The relatively long braincase is considered a primitive trait in cervids (Vislobokova, 1990), and the neurocranium of *A. latifrons* from Mundesley is more primitive than that of *A. gallicus*. The braincase is also relatively narrow for the frontal bones, attaining 46% of the frontal breadth.

The maximal span of antlers reached 2.5 m (Azzaroli, 1953). The distal palmation is fan-shaped, with long radially oriented tines. The length of the cylindrical beam and the palmated part of the antler roughly represents a proportion of 40:60 (Kahlke, 1969: Table XXVIII). The antler burr is perpendicular to the longitudinal axis of the pedicle and beam.

The metaconid and paraconid of P_3 are fused in the specimen from Mundesley (Azzaroli, 1953: Fig. 11) and in the lower mandibles from Süßenborn (Kahlke, 1969: Figs. 4, 5). Some isolated upper molars from Süßenborn are characterized by the weak presence of a lingual cingulum as seen in A. gallicus (Kahlke, 1969: Fig. 3). The protoconal fold is weak, especially in molars in the advanced stage of wear. In some molars, the posterior wing of the protocone includes a small enamel isle that resulted from the fusion of the protoconal fold with the posterior wing of the protocone (Kahlke, 1969: Fig. 3).

Distribution. The Middle Pleistocene of Europe (with exception of the Iberian Peninsula) and Western Siberia.

Alces alces (Linnaeus, 1758)

Synonymy:

1758 *Cervus alces* L.: Linnaeus, p. 92.

Diagnosis: see Flerov (1952)

Locus typicus: Southern Sweden.

Description. The cranial morphology of modern elks exhibits remarkable apomorphic characters, such as the premaxillary region's elongation and the loss of contact between the extremely long praemaxillae and nasals in all extant forms. Additionally, the nasal bones are short, the nasal aperture is sizable, and the vomer does not divide the aperture of the posterior nares (Franzmann, 1981; Breda and Marchetti, 2005). Nonetheless, nasopremaxillary contact has been maintained in the extinct Caucasian subspecies *A. alces caucasicus* Verestchagin, 1955. The angle between the parietal and occipital surfaces of the braincase is acute, while both sexes lack upper canines. Moreover, the upper molars in modern A. alces are characterized by a protoconal fold, which is still visible in M^3 (Lydekker, 1915: p. 231, fig. 35). According to Nikolsky and Boeskorov (2011), the European elk displays a higher frequency of advanced morphological variants of P^3, such as disjunction between protoconid and metaconid and between protoconid and hypoconid, when compared to elks from East Siberia.

The shape and development of antler palmation are known to vary within the species and even within the same elk population. While the antlers of the subspecies *A. alces caucasicus* and *A. alces cameloides* Milne-Edwards, 1867 (= *A. americanus cameloides* fide Boeskorov, 2001) are typically unpalmated, underdeveloped palmation has also been observed in other subspecies as individual variants. Unpalmated elk antlers follow a typical tree-pointed capreoline bauplan. The degree of palmation development in elks is influenced by individual age, quality of nutrition, and physical condition (Flerov, 1952). The antler beam is short and cylinder-shaped, much shorter than the breadth of the cup-shaped palmated portion of the antler. Among the elk species, the antlers of modern *A. alces* are less specialized and closer to the initial capreoline antler type. The area of distribution of *A. alces* includes the circumpolar boreal forests of Eurasia and Northern America (Flerov, 1952; Franzmann, 1981; Boeskorov, 2001).

Distribution. The earliest record of modern elk in Europe dates back to the lower Paleolithic, during the border between the Middle and Upper Pleistocene, as reported by Stefaniak (2007) or, according to Kurten (1968), during the Riss Glaciation (200-100 ky BP). Some authors, including Vörös (1985), Breda and Marchetti (2005), and Stefaniak (2007), suggest that "*Alces brevirostris* Kretzoi" from the Quaternary deposits of Solymar-Ördöglyuk Cave (Hungary), represents a transitional form between *A. latifrons* and *A. alces*.

Comments. According to Vörös (1985), *A. brevirostris* Kretzoi is characterized by longer nasal bones articulated with premaxillary bones and a relatively long antler beam. However, it is important to note that the species name "*Alces brevirostris* Kretzoi" is not valid because Kretzoi's manuscript containing the species description was never published and the original cranial material he studied has since been lost. Therefore, the brief report published by Vörös (1985), which describes the postcranial articulated skeleton with a figure of a shed antler, should be considered as the formal description of *Alces brevirostris* Vörös, 1985.

Genus *Rangifer* H. Smith, 1827

Diagnosis: see Flerov (1952).

Comments. The genus *Rangifer* is distinguished by a short and broad braincase, small upper canines, and large, complex antlers that are present in both sexes and highly variable in shape. In reindeer, the antlers typically have two anterior tines inserted in the lower part of the beam, a distinct posterior tine in the middle part of the beam, and multiple posterior crown tines that often form a small palmation. The nasal cavity of reindeer is divided by the vertical plate of the vomer at the posterior aperture of the nares (Vislobokova, 1990).

Type species: *Cervus tarandus* Linnaeus, 1758.

Composition: *Rangifer tarandus* (Linnaeus) (Middle Pleistocene – Holocene), *Rangifer* sp. nov. (Early Pleistocene of Isakovka-4southern Siberia: Bondarev et al., 2017).

Distribution: The earliest presence of reindeer in Europe is reported from the early Middle Pleistocene of Germany, France, and England (van Kolfschoten et al., 2011); however, only German reindeer fossils from Mosbach and Süßenborn were the subject of systematic and taxonomical study (Kahlke, 1963, 1969). The antlered reindeer braincase from the Middle Pleistocene of Mosbach sands is characterized by a very low position of the first (= ice) tine and the second (= ocular) tine and a simple branched distal crown. Kahlke (1963) described the reindeer from Mosbach and Süßenborn as the new subspecies *Rangifer arcticus stadelmanni* (= *R. tarandus stadelmanni* Kahlke, 1963 *fide* Croitor, 2010; van Kolfschoten et al., 2011) and assumed its close relationship with the barren-ground caribou of North America.

Rangifer tarandus (Linnaeus, 1758)

Synonymy:

1820 *Cervus guettardi* sp. nov.: Desmarest, p. 447.
1829 *Capreolus tournalii* [sp. nov.]: De Serres, p. ixv.
1829 *Capreolus leufroyi* [sp. nov.]: De Serres, p. ixv.
1829 *Cervus reboulii* [sp. nov.]: De Serres, p. ixv.
1846 *Cervus bucklandi* sp. nov.: Owen, p. 485, fig. 200.
1909 *Rangifer tarandus diluvia* ssp. nov.: Rutten, p. 71, tab. 2, fig. 10.
1914 *Rangifer tarandus fossilis* Owen: Sobolev, p. 1, pls. 1, 2.
1967 *Rangifer guettardi* (Desmarest): Bouchud, p. 237.
1983 *Rangifer tarandus guettardi* (Desmarest): Belan, p. 26.

Nomenclatural acts: Desmarest (1820) described a new species, *Cervus guettardi*, based on Cuvier's (1823) brief description of fossil reindeer antlers from Etampes. Bouchud (1967) later applied the name "*Rangifer guettardi*" to reindeer remains from the grotto near Foix (France) dated back to 7,100 years BC. The reindeer from Foix is of a comparable size to the reindeer represented by the fine complete skeleton from Villestofte (Denmark), which is also dated back to 11,000 years BC (Bouchud, 1966). Lydekker (1886) considered *Cervus guettardi* Desmarest a junior synonym of *Rangifer tarandus* (Linnaeus).

Owen (1846) described a new species, *Cervus bucklandi*, based on a basal fragment of a shed antler from the cave of Kirkdale. According to Owen, the antler from Kirkdale is very similar to *C. guettardi* but somewhat larger. Alekseeva (1980) reported a broad morphological variability of antlers and frequent underdevelopment of basal tines in Late Pleistocene reindeer from Southwestern Siberia. Therefore, *C. bucklandi* Owen, 1846 is another junior synonym of *R. tarandus*. Owen (1846) also reported a fine antlered skull of a reindeer from Bilney Moor near East Dereham, England. The antlers are rather thin and cylinder-shaped, resembling *R. tarandus* tarandus and *R. tarandus* stadelmanni from Mosbach. The reindeer from Bilney Moor represents a relatively small-sized form; however, only its breadth at pedicles (76.2 mm) is reported.

Sobolev (1914) reported finding some remains of reindeer in the Krasnoyarsk area of southern Siberia, identified as *R. tarandus fossilis* Owen (although the authorship granted to Owen is not correct) and of unknown geological age. The remains include those belonging to a small-sized form similar to *R. tarandus tarandus* (Sobolev, 1914: tab. 1, fig, 2), as well as those belonging to a larger, more robust form similar to the reindeer from Villestofte (ibidem, tab. 1, fig. 1).

Rutten (1909) based his extinct subspecies *R. tarandus diluvii* on fossil remains stored in the zoological museums of Utrecht and Leiden in the Netherlands. The main distinguishing character of Rutten's taxon is the asymmetric, underdeveloped, or missing subbasal antler tine (or "ocularspross," according to Rutten, 1909: 71). Therefore, *R. tarandus diluvii* Rutten, 1909 is similar to *C. bucklandi* Owen, 1846. The asymmetric and underdeveloped subbasal tine is common in reindeer, and *R. tarandus diluvii* Rutten, 1909 is most likely just another synonym of *Rangifer tarandus* Linnaeus.

The bibliographic data summarized by Bouchud (1966) demonstrates the inconsistency of reindeer systematics based on the shape of the antler beam. The unclear taxonomical criteria and poorly defined fossil Eurasian reindeer taxa create confusion and require thorough taxonomical and systematic study of fossil reindeer in the future

Diagnosis: see Flerov (1952)

Locus typicus: Sweden.

Description. The taxonomical challenges associated with fossil reindeer, as well as the well-known eco-morphological adaptability of the species, pose a significant obstacle to the study of fossil reindeer remains. As a result, students often classify reindeer fossils into general eco-morphological types, such as forest/woodland or tundra/barren-ground types (Bouchud, 1966; Ermolova, 1978; Alekseeva, 1980; Croitor, 2010a). However, this approach may oversimplify the matter, as the morphological variability of the vast number of reindeer fossils remains poorly understood. Several well-described subspecies of fossil reindeer have been identified in the western Palearctic.

Distribution. According to Geist (1998), the first dispersal event of reindeer in Eurasia occurred during the Riss Glaciation. The earliest occurrence of reindeer is documented in Süßenborn (Germany) where *R. arcticus stadelmanni* was recorded (Kahlke, 1969). The earliest presence of reindeer in Europe was also recorded in the early Middle Pleistocene of Germany, France, and England (van Kolfschoten et al., 2011); however, only German reindeer fossils from Mosbach and Süßenborn were the subject of systematic and taxonomical study (Kahlke, 1963, 1969). The modern distribution area of reindeer has a circumboreal character. During the Late Pleistocene, the area of distribution of reindeer ranged from the northern coast of the Black Sea to the Alps and Pyrenees, including the northern coast of the Iberian Peninsula (Flerov, 1952).

Rangifer tarandus hibernicus Scharff et al., 1917

Scharff et al. (1917: 63) established *R. tarandus hibernicus* as a subspecies of extinct reindeer from Ireland based on a relatively complete antlered skull from the Ashbourne bog (figured in Carte, 1864) and fragmented osteological material from Castlepook Cave (Ireland).

While following the diagnostic characters for the modern reindeer proposed by Lönnberg (1909), Scharff et al. (1917) provided only measurements and a morphological description of the nasal bones of the Ashbourne skull. The nasal bones are flat, similar to those of *R. tarandus tarandus* from Sweden, with a relatively large nasal cavity and a nasal bone breadth and length of 16 mm and 131 mm, respectively. The antlers of the Ashbourne skull are large and richly branched, with main beams and basal tines terminating in broad palmations resembling those of the reindeer from Villestofte. Bouchud (1966) dated the Ashbourne skull to the Allerod oscillation (10,000 years BC).

Rangifer tarandus tournalii (De Serres, 1829)

Synonymy:

1829 *Capreolus tournalii* [sp. nov.]: De Serres, p. ixv.

Diagnosis: a comparatively large form of reindeer similar in size to modern forest reindeer. Antlers are compressed lateromedially. Cheek teeth are moderately large.

Holotype: the proximal fragment of the right antler with a pedicle and a part of the frontal bone (Fig. A.12, Tab. A.5). The specimen is stored in the National Museum of Natural History, Paris.

Locus typicus: Tournal (= Bize) Cave (Aude, Southern France).

Stratum typicum: the Late Pleistocene, possibly the older Mousterian or Aurignacian units of the Tournal Cave.

Description. The antler type is from a male reindeer that was large in size, but the specimen is deformed and poorly preserved, with partial damage to the antler burr. The pedicle is short and robust, with regular circular cross-sections in the pedicle and basal part of the antler. The first ramification is high above the burr, and the specific basal tine is not developed. The antler becomes compressed lateromedially in the ramification area, and the first antler tine is flattened.

The complete series of lower premolars in the left mandible fragment measures 44.0 mm, slightly larger than modern *R. tarandus tarandus* (L P_2-P_4 = 39.7 mm and 36.4 mm from the Natural History Museum of London), but smaller than *R. tarandus constantini* from the Late Pleistocene of Cosăuți (L P_2-P_4 = 47.0 mm and 47.6 mm; IZC) and Rașcov-8 (47.7 mm). The size of the premolar series from the Tournal Cave is similar to the large forest form of reindeer from the Late Pleistocene of Duruitoarea Veche (45.4 mm) and Brânzeni-1 (45.7 mm; IZC). The upper fourth premolar measurements from the Tournal Cave are also close to Brânzeni-1 and significantly larger than the sample from Jaurens, France (29 300 – 32 630 years BP: Valli, Guérin [2000]), which is roughly coeval with Brânzeni-1.

The talus from the Tournal Cave measures 45.0 mm in maximum height, 29.4 mm in distal breadth, and 22.8 mm in distal anteroposterior measurement, which corresponds to a female of a relatively large form of reindeer based on the size of the dentition. The measurements are similar to the largest males from Cosăuți and smaller females from Duruitoarea Veche.

Rangifer tarandus constantini Flerov, 1934

Synonymy:

1934 *Rangifer constantini* sp. nov.: Flerov, p. 239, pl. 8.

Diagnosis: see Flerov (1934)

Holotype: a partially preserved male (?) skull from the collection of the Geological Institute, Moscow (lost).

Locus typicus: the Late Paleolithic site of Malta (Irkutsk, Siberia).

Stratum typicum: Late Pleistocene, "Solutrean age" *fide* Flerov (1934); ca. 16 000 years BC *fide* Bouchud, 1967).

Description. This fossil subspecies of reindeer is the most well-defined, characterized by a narrow and high muzzle with a ratio of 57.9% between the cranial breadth at P^2 and the rostral height at rhynion, an elongated head, and relatively large teeth, larger than any other modern or fossil reindeer form. The most notable characteristic is the size of the upper cheek teeth, with the M^1-M^3 series measuring 56.5 mm in length. The nasal bone length of *R. tarandus constantini* is shorter than that of *R. tarandus hibernicus*, but longer than the reindeer from Foix and Villestofte (Bouchud, 1967). Although Bouchud (1966) defined *Rangifer constantini* as a forest reindeer, the relatively small body size of the reindeer from Malta, its short limb bones, simple long antlers with small palmations, and large cheek teeth define *R. tarandus constantini* as an open-landscape grazing form (Croitor, 2010).

R. tarandus constantini exhibits an extreme adaptation to grazing in an open dry periglacial environment. Its food habits were likely similar to those of the fossil reindeer from Alaska, which displayed heavy occlusal tooth wear in young and adult animals due to a very abrasive diet (Rivals and Solounias, 2007). Unlike modern reindeer, *R. tarandus constantini* has a relatively small nasal cavity, suggesting that Paleolithic reindeer had not yet evolved adaptations to cold air breathing (Flerov, 1952). An increased nasal cavity warms and moistens the air before entering the trachea and lungs. Muzzle breadth is correlated with nasal cavity volume, with modern Arctic reindeer having the highest recorded maximal volume of the nasal cavity (Flerov, 1952; Sokolov, 1995).

Distribution. The remains of small-sized reindeer with large teeth similar to *R. tarandus constantini* have been found at several Late Paleolithic sites, including Kostenki in European Russia (20-30 kya), Cosouti and Rascov-8 in Moldova (11-21 kya), and l'Aven des Planes in southern France (during the final stage of the Würm glaciation). These sites provide evidence for the westward dispersal of *R. tarandus constantini* during the Last Glacial phase in Europe.

Rangifer tarandus stadelmanni Kahlke, 1963

Synonymy:

1963 *Rangifer arcticus stadelmanni* ssp. nov.: Kahlke, p. 277, fig. 1.
1984 *Rangifer tarandus stadelmanni* Kahlke, 1963: Willemsen, p. 59, fig. 3.

Nomenclatural acts: According to Kahlke (1963), the fossil reindeer from Mosbach is morphologically similar to the modern barren-ground caribou of North America and was described as a subspecies of *Rangifer arcticus* Richardson, 1829. Flerov (1952) considered North American barren-ground reindeer to be a subspecies of reindeer, *R. tarandus arcticus*. Willemsen (1984) included Kahlke's reindeer as a subspecies in *R. tarandus*.

Diagnosis: see Kahlke (1963).

Holotype: antlered braincase (Kahlke, 1963).

Locus typicus: Mosbach, Germany

Stratum typicum: Middle Pleistocene of Mosbach sands.

Description. The knowledge about this particular form of reindeer is limited. However, based on the available evidence, it can be inferred that the antlered reindeer braincase from the Middle Pleistocene has some distinctive features. Notably, the first (= ice) tine and the second (= ocular) tine are positioned very low, and the distal crown has a simple branching pattern. Additionally, there is no significant development of distal palmations.

Distribution: Middle Pleistocene of Germany.

3.2. Conclusions to Chapter 3

1) Taxonomic revision and morphological examination of fossil deer from the Late Miocene in the western Palearctic region have revealed the early evolutionary stage of telemetacarpal deer. This stage represents an initially rich early evolutionary radiation of the subfamily Capreolinae, comprising 9 genera (Croitor, 2021). However, by the beginning of the Pliocene, the early evolutionary radiation of Capreolinae had rapidly declined, leaving only two genera (*Procapreolus* and *Croizetoceros*) in the western Palearctic (Croitor, 2021).

2) The representatives of the early evolutionary radiation of telemetacarpal deer are characterized by relatively advanced dentition morphology and exhibit all evolutionary stages of antlers, ranging from simple two-pointed antlers to multitined palmated antlers. Additionally, the

Palaeomeryx fold in lower molars is one of the most characteristic features of early representatives of the subfamily Capreolinae (Croitor et al., 2020; Croitor, 2021).

3) Some early representatives of the subfamily Capreolinae were characterized by a holometacarpal condition. This morphological condition was marked by the partial reduction of the upper portions of lateral metacarpals and their robust functioning distal articulations, as recorded in *Metadicrocerus variabilis* (Aleksejev, 1913) (Croitor, 2021).

4) The evolution of modern telemetacarpal genera of the Palearctic region (*Capreolus*, *Alces*, and *Rangifer*) is linked to the eastern part of the Palearctic. These genera dispersed into the western Palearctic during the Pleistocene, following the extinction of the last archaic western telemetacarpal genus, *Croizetoceros* (Croitor, 2018b).

4. SYSTEMATIC DIVERSITY OF PLESIOMETACARPAL DEER (SUBFAMILY CERVINAE GOLDFUSS, 1820) IN WESTERN PALEARCTIC

4.1. Subfamily Cervinae Goldfuss, 1820

Genus *Praemuntiacus* Croitor, Zakharov and Mararescul, 2020

Diagnosis: The body size of the animal is similar to that of modern *Muntiacus*. The antlers are simple with two points, and their bifurcation is positioned low (the bifurcation height does not significantly exceed the anteroposterior diameter of the antler above the burr). The anterior tine is strongly developed and can vary in length. The posterior tine is the main axis of the antler and can grow up to approximately 10 cm in length. The cross-section of the antler branches typically has a triangular shape due to the well-developed longitudinal ribs, which include the anterior, medioposterior, and lateroposterior ribs. The pedicles are relatively short and robust, and they may be more or less divergent. The frontal bones are relatively broad, approximately 20% broader than in Muntiacus, and they lack sharp bony ridges. In males, the upper canines are large, long, and sabre-shaped. The lower fourth premolar is primitive (not molarized). The upper molars lack an additional protoconal fold, while the lower molars lack the *Palaeomeryx* fold.

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).

Praemuntiacus pidoplitschkoi (Korotkevich, 1964)

Synonymy:

1964 *Eostyloceros pidoplitschkoi* sp. nov.: Korotkevich, p. 807, fig. 1.
1965 *Muntiacus pliocaenicus* sp. nov.: Korotkevich, p. 107, fig. 2.
1968 *Muntiacus polonicus* sp. nov.: Czyżewska, p. 582, pl. VIII, figs. 3, 4.
2003 *Eostyloceros* cf. *pidoplitschkoi* Korotkevich, 1964: Abbazzi and Croitor, p. 577, fig 3.
2016 *Muntiacus* cf. *polonicus* Czyżewska, 1968: Feifar et al., p. 4, fig. 2.
2018 *Euprox pidoplitschkoi* (Korotkevich, 1964): Croitor, p. 53, fig. 12.

Nomenclatural acts: The Pliocene muntjac-like cervids of Europe were placed in the Asian genera *Eostyloceros* and *Muntiacus* (Korotkevich, 1964b, 1970; Czyżewska, 1968; Fejfar, et al., 1990). Zdansky (1925) established the genus *Eostyloceros*, with the type species *Eostyloceros blanvillei*, based on antlers with two points from Tertiary deposits in China. Deng et al. (1914) identified a new species, *Eostyloceros hezhengensis*, as a basal form within the *Eostyloceros*, *Paracervulus*, *Euprox*, and *Lucentia* group. In the same publication, Deng et al. (2014) proposed that *Eostyloceros*, as traditionally understood, is paraphyletic. Mennecart et al. (2017) excluded *Eostyloceros* from the so-called crown Cervidae and suggested its intermediate phylogenetic position between *Dicroceros* and *Muntiacus*. Although purportedly related to *Muntiacus*, *Euprox furcatus* is unambiguously placed in the "stem Cervinae" group (Mennecart et al. 2017). According to Mennecart et al. (2017), *E. furcatus* diverged from the main Cervinae phylogenetic branch before the dichotomy between muntjacs and large cervines.

Korotkevich (1964b) described a small two-pointed antler attached to a short pedicle from the Pliocene of Trifești (misspelled as Trifoneşti by Korotkevich), Southern Moldova, as a muntiacine deer *Eostyloceros pidoplitschkoi*. According to Korotkevich (1964), the simple antler structure combined with the short pedicle align this cervid form with the genus *Eostyloceros* Zdansky, 1925 from the Late Tertiary of China. Later, Korotkevich (1970) assigned a series of similar antlers from the Early Pliocene of Kuchurgan, Ukraine to this species. From the same Kuchurgan deposits, Korotkevich (1965b) described another muntjac-like deer *Muntiacus pliocaenicus* based on a few poorly preserved antlers with frontal bones characterized by slightly longer pedicles and frontal bony ridges, which according to Korotkevich's interpretation, is a diagnostic character that approaches the cervid remains in question to modern *Muntiacus*. Korotkevich (1965b, 1970) considered these frontal bony ridges in *Muntiacus pliocaenicus* as essential diagnostic characters that link this species to modern Muntiacus.

Croitor (2014, 2018b) tentatively included *E. pidoplitschkoi* and *M. pliocaenicus* in the genus *Euprox*, since the morphology of their antlers shows a strong resemblance with Miocene *E. furcatus*. However, the revision of the sample studied by Korotkevich (1964b, 1965b, 1970) and new rich material from the Priozernoe site (Cuciurgan River Valley) demonstrated that the measurements of antlers and pedicles of *Eostyloceros pidoplitschkoi* and *Muntiacus pliocaenicus* most likely represent different stages of ontogenetic development of the same species (Croitor et al., 2020). The specimens described by Korotkevich (1970) as *E. pidoplitschkoi* and *M. pliocaenicus* represent a homogenous sample. The material of muntjac-like deer from Kuchurgan is incomplete, and one can observe that *E. pidoplitschkoi* and *M. pliocaenicus* are distinguished only by a slight difference in their pedicle length, and most probably represent different ontogenetic stages of the same cervid form (Croitor, 2014). Therefore, these species' names are considered synonyms.

Czyżewska (1968) described a juvenile mandible from the Early Pliocene of Węże-1 and established a new species, *Muntiacus polonicus*. Direct comparison of this species with M. pliocaenicus was not possible due to the use of different skeletal parts (Croitor and Stefaniak, 2009). As *M. polonicus* is from the roughly coeval Early Pliocene fauna of Węże-1, this species name is also considered a synonym of *P. pidoplitschkoi* (Korotkevich, 1964) in this study.

Diagnosis: This species is a small-sized deer, similar in body size to the modern Muntiacus reevesi. The antlers are two-pointed and may deviate laterally from the pedicle axis. The surface of the medial side of the antler in the area of bifurcation is often pearled. The pedicles are relatively short and moderately diverged. There are no sharp frontal bony ridges.

Holotype: the right antler attached to a portion of frontal bone Nr. 5634 from Trifești is housed in the paleontological collection of the Paleontological department of the National Museum of Natural History, Kyiv (Fig. A.13). The specimen likely belongs to an older individual or a more evolved form than the samples from Cuciurgan River Valley.

Locus typicus: as indicated by Korotkevich (1964b), the type locality of *P. pidoplitschkoi* is "Trifonești, Moldova, Bessarabian Sands". However, according to Godina and David (1973), the fossiliferous outcrops of "Bessarabian sands" near Trifonești do not exist in Moldova. Therefore, it is likely that the antler described by Korotkevich (1964b) comes from the Trifești site (also known as Trifești-2), which is situated near Trifestii Noi village, Cahul District, as reported by Alekseeva (1977).

Stratum typicum: “Bessarabian Sands” (Korotkevich, 1964b); the Early Pliocene, MN15, the Carbolian alluvium (Vangengeim et al., 1998).

Description. The antlers are two-pointed with a low position of bifurcation. The posterior tine is stronger and longer than the anterior one and is oriented along the axis of the pedicle. The antler surface is sculptured with sharp and deep ridges and furrows, and a specific rugosity is often seen on the medial surface of the antler base. The cross-section of the antler tines is often sub-triangular, as seen in modern *Muntiacus*. However, the antlers and pedicles of *P. pidoplitschkoi* are significantly more robust than those of *Muntiacus*.

The weak roll-shaped structures on the lateral side of the frontal bones between pedicles and orbits are common for cervids and do not correspond to the sharp bony ridges characteristic of modern *Muntiacus*. These ridges are a specific adaptation for eye protection during intraspecific male combats and represent a particular adaptation of the genus *Muntiacus*.

The mandible from Węże-1 (Nr. 99-Węże-1, IZW) is almost identical in size and shape to modern Muntiacus. The DP_3 is characterized by the anteroposteriorly elongated metaconid, which distinguishes this specimen from modern Muntiacus characterized by a small simple metaconid. DP_4 is supplemented with two ectostylids. The mandible from Węże-1 is also distinguished from the Middle and Late Miocene *Euprox* by the absence of the *Palaeomeryx* fold and smaller size. The ectostylids of lower molars are well-developed. The length of the lower tooth row (deciduous teeth and molars) is about 62.3 mm, and the occlusal length of the molar series amounts to 35.9 mm.

The upper molar (M^3) Nr. 254 from Węże-1 is partially destroyed. The entostyle is not developed, but the additional enamel fold of the hypocone is well-developed. The metaconid has a particularly well-expressed metastyle (the posterior labial rib) and the middle labial rib. This character approaches the specimen under study to modern muntjacs, which show a similar morphology. The length of the molar crown is 9.8 mm (measured at the tooth base), and the basal labiolingual breadth of the tooth amounts to 11.5 mm.

Distribution. Most of the remains of *P. pidoplitschkoi* come from the Ruscinian fauna of Poland, Romania, Bulgaria, Ukraine and Moldova (MN 14 and MN 15) (Radulescu et al., 2003; Croitor and Stefaniak, 2009). The youngest remains of *P. pidoplitschkoi* are reported from MN 16a of Slovakia (Fejfar et al., 1990). The earliest remains of *P. pidoplitschkoi* are known from the earliest stage of the Ruscinian or even the end of MN13 in Bulgaria (Spassov, 2005). The exact age of the shed antler of *P. pidoplitschkoi* from Montopoli (Italy) remains unclear (Abbazzi and Croitor, 2003).

Genus *Metacervocerus* Dietrich, 1938

Nomenclatural acts: In 1938, Dietrich proposed the subgenus *Cervus* (*Metacervocerus*) to group Late Pliocene small-sized *Axis*-like cervines of Europe with simple three-pointed antlers. Later, Samson et al. (1970) elevated *Metacervocerus* to the generic level.

Diagnosis: three pointed antlers are characterized by the more or less high position of the first ramification and the parasagittal orientation of the second bifurcation. The posterior branch of the second bifurcation is stronger and longer that the anterior one and represents a continuation of the antler beam. The cross-sections of the beam and tines are circular. The antler surface is not pearled. Pedicles are moderately long, somewhat divergent and sloped backwards from the face. The protocone in upper molars is not bofurcated. P_4 is unmolarised.

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.

Metacervocerus pardinensis (Croizet and Jobert, 1828)

Synonymy:

1853 *Cervus* (*Rusa*) *pardinensis* Croizet and Jobert, 1828: Pomel, p. 106.
1859 *Cervus* (*Axis*) *pardinensis* Croizet and Jobert, 1828: Gervais, p. 84.
1878 *Cervus suttonensis* sp. nov. (partim.): Dawkins, p. 412, fig. 7.
1938 *Cervus* (*Metacervocerus*) *pardinensis* Croizet and Jober, 1828t: Dietrich, p. 261.

1970 *Cervus* [*sensu lato*] *pardinensis* Croizet and Jobert: Heintz, p. 133.
1970 *Metacervocerus pardinensis* (Croizet and Jobert, 1828): Samson et al., p. 66.
1990 *Cervus* (*Rusa*) *pardinensis* Croizet and Jobert, 1828: Vislobokova, p. 154.
1992 *Pseudodama pardinensis* (Croizet and Jobert, 1828): Azzaroli, p. 4.
2005 *Dama pardinensis* (Croizet and Jobert, 1828): Pfeiffer, p. 52.

Nomenclatural acts: Croizet and Jobert (1828) illustrated remains of a deer, including a complete shed antler, a distal portion of an antler, fragments of mandibles, and postcranial bones, on Plate XI titled "Cerfs fossils de la montagne de Perrier et de Malbatu (premier sous-genre)". Pomel (1853) proposed the scientific name *Cervus pardinensis* and a diagnosis that corresponds to the above-mentioned figure published by Croizet and Jobert (1828). Pomel (1853) credited Croizet and Jobert (1828) as the authors of the species. Heintz (1970) conducted the first revision of the species and designated the antler figured by Croizet and Jobert (1828) as the neotype.

Diagnosis: The antler beam is rather straight; the ramification angles are acute. Upper molars and P^4 are supplemented with a well-developed cingulum.

Neotype: a left shed antler, MNHN (Croizet and Jobert, 1828: pl. XI, fig. 4; Heintz, 1970: p. 71, fig. 142, pl. VIII, fig. 6a, b)

Locus typicus: Les Etouaires (= Perrier-Etouaires), Puy-de-Dome, France (Heintz, 1970).

Stratum typicum: Alluvial deposits of Les Etouaires, Late Pliocene, Early Villafranchian, MN16.

Description. This is a small cervid with an estimated body mass of about 60 kg and simple three-pointed antlers (Fig. A.14). The circular antler base of the neotype antler has a burr diameter of 49.0 mm. The beam above the burr is slightly compressed from the sides, with a DAP x LDM of 38.6 x 35.1 mm. The antler beam gently curves backward and sideward, deviating slightly from the burr. The first tine is located at 70.0 mm (if measured from the medial side) or 65.8 mm (lateral side) from the burr. Above the first ramification, the antler beam is cylindrical with a DAP x LDM of 29.1 x 27.7 mm. The distal bifurcation is in the parasagittal plane, and the posterior tine of the distal bifurcation is stronger and longer than the anterior one. The total length of the antler is over 56 cm.

Additional material provides the following characteristics: the pedicles are moderately long, with the medial length similar to the transversal diameter. They are slightly compressed in the anteroposterior direction and slope backwards from the face, similar to modern *Hyelaphus* or *Rusa*. The dentition is rather primitive, with the upper molars characterized by a very oblique lingual wall and supplemented with a strong cingulum. The angle between the lingual and labial walls in M^2 is wider than 40°. The morphology of P_4 is primitive.

Distribution. The oldest remains of *Metacervocerus pardinensis* come from the Late Ruscinian (MN15) faunas of Moldova (Luceşti, Dermenji, Brânza) (Vislobokova, 2005) and Bulgaria (Musselievo) (Spassov, 2005). Some poorly preserved remains that can be attributed to *M. pardinensis* are also reported from MN15b faunas of Braşov Depression, Romania (Căpeni, Vârghiş) (Radulescu et al., 2003) and Poland (Węże-2) (Stefaniak, 1995). Younger remains have been found in Romania (Tuluceşti, Cernăteşti, Groserea, Covrigi) (Radulescu et al., 2003; Radulescu, 2005) and Slovakia (Hajnacka) (Sabol, 2003), dated to MN16a, which is similar in age to *M. pardinensis* remains found in Vialette, France. The youngest remains of this species have been identified at the type locality of Etouaires (France) and the Red Crag Nodule Bed (England), which correspond to MN16b (Lister, 1999). The known distribution of this species ranges from France and England in the west to Poland, Moldova, and Bulgaria in the east.

Metacervocerus rhenanus (Dubois, 1904)

Synonymy:

1904 *Cervus* (*Axis*) *rhenanus sp. nov.*: Dubois, p. 219, fig. 2.
1941 *Cervus philisi sp. nov.*: Schaub, p.264, pl. 17.
1952 «*Cervus*» *perolensis sp. nov.*: Bout and Azzaroli, p. 51, fig. 8.
1990 *Cervus* (*Rusa*) *philisi* (Schaub, 1941): Vislobokova, p. 154.
1990 *Cervus* (*Rusa*) *perolensis* (Azzaroli, 1952): Vislobokova, p. 154.
1992 *Pseudodama rhenanus* (Dubois, 1904): Azzaroli, p. 4.
1992 *Pseudodama perolensis* (Azzaroli, 1952): Azzaroli, p. 4.
1992 *Cervus ichnoceros sp. nov.*: Boeuf *et al.*, p. 166, pl. III, Fig. a, 1-2.
1992 Cervus *rhenanus* (Dubois, 1904): Spaan, p. 23, fig. 8.
1997 *Dama* (*Pseudodama*) *rhenana* (Dubois, 1904): Pfeifer, p. 38.
2001 *Metacervoceros rhenanu*s (Dubois, 1904): Croitor and Bonifay, p. 138, figs. 13-17.

Nomenclatural acts: In 1904, Dubois introduced the species *Cervus* (*Axis*) *rhenanus* for a small deer found in Tegelen. However, the original publication of the species name lacked a description, and only included a figure of the type specimen. According to Spaan (1992), *Cervus philisi* Schaub, 1941 is a junior synonym of *Cervus rhenanus* Dubois, 1904. Later, Croitor and Bonifay (2001) included *Cervus rhenanus* in the genus *Metacervocerus* Dietrich, 1938.

Diagnosis: The braincase is elongated and unflexed, with slightly convex parietal bones. The pedicles are moderately long and slope backwards, while the anterior part of each frontal bone is slightly swollen. The preorbital fossae and ethmoidal openings are large, and the orbitofrontal region is short, with the anterior edge of the eye sockets reaching the level of M^2. The bullae timpani are large and rounded, and the basioccipital bone is broadened at the pharyngeal tuberosities, giving it a bell-like shape. The processus angularis is well-defined, and the diastema of the lower mandible is slightly longer than the lower molar series. The angle between the lingual and labial walls of the upper molars is more than 40º, and upper canines are absent. The lower fourth premolar is primitive, and the angle of the first ramification varies from 100º to 60º.

Holotype: the unshed complete left antler Ha 15777 (TMH) is the holotype of the species (Spaan, 1992: fig. 8).

Locus typicus: Tegelen, the Netherlands.

Stratum typicum: clays of Tegelen, Late Tiglian, Early Pleistocene.

Description. The antlers of this species are long, thin, and three-pointed. In the skull CEY-2-2318 from Ceyssaguet (Fig. A.15), the total antler length is 760 mm (right) and 767 mm (left). The distance from the antler base to the top in the same specimen is 710 mm (right) and 732 mm (left). The distance between the tops of the antlers is 565 mm, and the proximal parts of antler beams form an angle of 70°. The middle third of the antlers is bow-shaped and more divergent, while the distal portions are more or less parallel to each other. The angle of the first ramification is approximately 60°, and the basal tine is situated at a certain distance from the burr. The distal bifurcation is oriented in the parasagittal plane and formed by the second tine inserted on the anterior side of the beam. The antler beam becomes compressed laterally in the area of the distal bifurcation, and the surface of the antler may be concaved from the sides in this area. The angle of distal bifurcation is approximately 40-45°. The transversal section of antler tines is circular, and the antler surface is pearled and sculptured with longitudinal ribs and furrows.

The angle of the first ramification of the antler is a variable characteristic and ranges from 60° to 100° (Croitor, 2006b). In the sample from Ceyssaguet, the height of the first ramification varies from 41.6 mm to 83.5 mm

. The frontal bones have a concave profile at the level of the anterior half of the orbits, with the anterior part of each frontal bone slightly swollen. The pedicles are long, slightly dorso-ventrally compressed, and slope backward from the face. The anterior edge of the orbits projects down to M^2, while the nasal bones are comparatively long and extend behind the line connecting the anterior edges of the orbits. The preorbital fossae and ethmoidal openings are large and deep, with the border between the ethmoidal openings and the nasal bones varying in length from sample to sample. The articulation between the nasal and premaxillary bones is long, measuring 23 mm in the skull Nr. 210638, PMUL, much longer than in modern *Dama dama* and similar to *Cervus*. The braincase is elongated, unflexed, and not rounded as in *Dama*, but rather long as in *Axis* and longer than in *Cervus* and *Dama*. The bullae tympani are rounded and smooth but not as large as in *Dama*. The face length, measured from the anterior edge of the orbits to prosthion, is 56.9% of the condylobasal length in the female skull Nr. 210638, which is relatively longer than in *Hyelaphus porcinus* (51.3 – 54.7%, n=5) and *Cervus nippon* (52.8 – 55.1%, n=3) but falls within the variation range of *Axis axis* (50.4 – 57.8%, n=4). The cranial proportions of *M. rhenanus* and such morphological peculiarities as the long pedicles and rather large and rounded bullae tympani are similar to modern *Axis*. However, *M. rhenanus* shows a derived character of long, caudally extended nasal bones unlike *Axis*.

The mandible Nr. 209564 (PMUL) from Sénèze is distinguished by a rather long diastema, which is slightly longer than the series of lower molars. It is comparatively longer than in *Cervus nestii*, *Cervus nippon*, and *Dama dama*, but shorter when compared to *Hyelaphus porcinus* and *Cervus elaphus*. The ratio between premolars and molars varies from 61.4% to 65.8% (n=7; M=63.5%). The processus angularis is strong.

The hypocone and protocone of P^2 are distinct. The hypocone of P^2 has an internal enamel fold. The lingual wall of P^3 has a vertical groove that separates the merged hypocone and protocone. The hypocone of P^3 also has an internal enamel fold. There is no separation of hypocone and protocone in P^4.

The upper molars may display a weak cingulum and are typically supplemented with a protoconal enamel fold and an eperon. However, only three specimens (all M^3) from the sample at Sénèze exhibit a weak continuous cingulum, while in the majority of remains (22 specimens), the cingulum is either interrupted or completely reduced. The cingulum appears to be more frequent in the sample from Vallonnet (RMPM). Individual variation in P_4 in the sample from Ceyssaguet is characterized by the variable shape of metaconid that in some cases is extended caudally and is merged with entoconid. However, the contact between metaconid and paraconid has never been observed. The crown of I_1 is wide and triangle-shaped with an extended and acute lateral angle, while I_2, I_3, and C are smaller and very narrow (Croitor, 2006b).

The upper isolated molar M^3 R12079 from Vallonnet (RMPM) is characterized by a very oblique lingual side that forms an angle of 45° with the labial surface of the tooth and a clear cingulum that borders the basal part of the protocone. This combination of features is found in several isolated teeth. Furthermore, the left hemimandible Nr. 416 (RMPM) is characterized by a primitive P_4.

Distribution. *Metacervocerus rhenanus* persisted throughout the Early Pleistocene with little change from its first occurrence 2.5 million years ago in Saint-Vallier, France, to its last record 0.9 million years ago in Vallonnet, France. It was distributed throughout Spain, France, the Netherlands, Romania, and Greece (Croitor and Bonifay, 2001), but is absent from the Early Pleistocene of Italy.

Genus *Praeelaphus* Portis, 1920

Nomenclatural acts: Portis (1920: p. 133) proposed the subgenus *Cervus* (*Praeelaphus*) for three Early Villafranchian deer species from France: *Cervus arvernensis* Croizet and Jobert, 1828, *Cervus perrieri* Croizet and Jobert, 1828, and *Cervus etueriarum* Croizet and Jobert, 1828, which were found in Perrier. Grubb (2000) suggested that *Praeelaphus* Portis, 1920 might be synonymous with *Metacervocerus* Dietrich, 1938, since Portis (1920) considered that *C. pardinensis* is a junior synonym of *C. perrieri*. However, this is not the case, as *Praeelaphus* and *Metacervocerus* are based on two valid species: *C. perrieri* and *C. pardinensis*, respectively. Heintz (1970) placed *C. perrieri* in the arbitrary group *Cervus sensu lato*, suggesting that its systematic position is uncertain. Croitor (2012) proposed including several archaic Pliocene and Pleistocene deer species from western Eurasia that belong to the early evolutionary radiation of the Cervinae group in the genus *Praeelaphus* Portis, 1920, and indicated *C. perrieri* as the genotype.

Diagnosis: Deer of the size of modern European red deer and fallow deer. Pedicles of moderate length (posteromedial length of the pedicle in adult males does not normally exceed its diameter) and slightly compressed anteroposteriorly. Fully grown antlers are large relative to the animal size, four-pointed. The first tine is situated above the burr at a distance larger than the diameter of the antler base. The antler beam often forms well-expressed flattened extensions in the areas of ramification. The transversal section of the beam below the second tine is not regular, often pyriform or ovoid. The beam above the second tine is significantly compressed and forms an extended flattening with frontal or parasagittal orientation. Correspondingly, the distal bifurcation may be oriented in the frontal or parasagittal plane. The dentition is primitive: P_4 is generally simple, with a low degree of molarization, and the lower premolar series is relatively long compared to molars and longer than in *Cervus* and *Dama*.

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 Europe and Transcaucasia.

Praeelaphus perrieri Croizet et Jobert, 1828

Synonymy:

1828 premier sous-genre: Croizet and Jobert, pl. II, figs. 1-16, pl. IV, figs. 1-9.
1853 *Cervus* (*Strongyloceros*) *perrieri* Croizet and Jobert, 1828: Pomel, p. 104.
1853 *Cervus* (*Strongyloceros*) *issiodorensis* Croizet and Jobert, 1828 (partim.): Pomel, p. 105.
1853 *Cervus* (*Rusa*) *etueriarum* Croizet and Jobert, 1828: Pomel, p. 106.
1853 *Cervus* (*Rusa*) *rusoides* Nob.: Pomel, p. 106.
1878 *Cervus cylindroceros* sp. nov.: Dawkins, p. 415, fig. 12.
1884 *Cervus* (*Elaphus*) *issiodorensis* Croizet: Deperet, p., 263, pl. VI, fig. 6.
1884 *Cervus* (*Elaphus*) *etueriarum* Croizet: Deperet, p. 265, pl. VI, fig. 5.

1884 *Cervus* (*Elaphus*) *perrieri* Croizet: Deperet, p. 268, pl. 6, fig. 7.
1920 *Cervus* (*Praeelaphus*) *arvernensis* Croizet and Jobert, 1828: Portis, p. 133.
1920 *Cervus* (*Praeelaphus*) *etueriarum* Croizet and Jobert, 1828: Portis, p. 133.
1920 *Cervus* (*Praeelaphus*) *perrieri* Croizet and Jobert, 1828: Portis, p. 134.
2012 *Praeelaphus perrieri* (Croizet and Jobert, 1828): Croitor, p. 223.

Nomenclatural acts: Pomel (1853) published the first brief description of deer species *Cervus perrieri*, *Cervus etueriarum*, and *Cervus issiodorensis* based on fossil remains from Perrier, which were figured by Croizet and Jobert (1828). Dawkins (1878) demonstrated that morphological differences between *C. perrieri* and *C. issiodorensis* have the character of individual variation. This opinion was confirmed by Heintz (1970). According to Heintz (1970), *C. etueriarum* is based on juvenile antlers of *C. perrieri*, however, he did not find any antler in the collection of MNHN that rigorously corresponds to the specimen figured by Croizet and Jobert (1828). Some other remains ascribed to *C. issiodorensis*, in the opinion of Fejfar et al. (2016: fig. 7, b), belong to *Metacervocerus pardinensis*. *C. arvernensis*, which also was included by Portis (1920) in *Praeelaphus*, apparently, is a name created by Bravard but never published and described afterwards (Lesson, 1836: 259). Possibly, the name *C. arvernensis* was given to the poor fragment of antler with low insertion of the basal tine (Croizet and Jobert, 1828: pl. XI, fig. 1), and most probably, it also falls within the individual variation of *C. perrieri* (Ctoitor, 2017). Pomel (1853: 112) did not give a definition for this species name, since, in his opinion, "*C. arvernensis* est connu par des bois trop irréguliers pour ne pas être anomaux; l'espèce est incertaine".

Heintz (1970), who published the first revision of *C. perrieri*, could not find any specimen in the collection of MNHN that corresponds rigorously to the specimen figured by Croizet and Jobert (1828: pl. IV, fig. 1) and chose a neotype that better corresponds to the original figure and possibly represents the same specimen. There are two other specimens labelled as types of *C. issiodorensis* Croizet and Jobert, 1828 and stored in the collection of PMUL: the basal part of a right shed antler Nr. 211214 and the right astragallus Nr. 211205.

Diagnosis: Deer of the size of modern European red deer and fallow deer. Pedicles of moderate length (posteromedial length of the pedicle in adult males does not normally exceed its diameter) and slightly compressed anteroposteriorly. Fully grown antlers are large relative to the animal size, four-pointed. The first tine is situated above the burr at a distance larger than the diameter of the antler base. The antler beam often forms well-expressed flattened extensions in the areas of ramification. The transversal section of the beam below the second tine is not regular, often pyriform or ovoid. The beam above the second tine is significantly compressed and forms an extended flattening with frontal or parasagittal orientation. Correspondingly, the distal bifurcation may be oriented in the frontal or parasagittal plane. The dentition is primitive: P_4 is generally simple, with a low degree of molarization, and the lower premolar series is relatively long compared to molars and longer than in *Cervus* and *Dama*.

Neotype: a right almost complete antler with a part of the frontal bone, MNHN (Heints, 1970: fig. 261, pl. XV, fig. la, b), that possibly is a part of the antlered frontlet figured by Croized and Jobert (1828: pl. IV, fig. 1).

Locus typicus: Les Etouaires, Puy-de-Dôme, France

Stratum typicum: alluvial deposits of Etouaires, Lower Villafranchian.

Description. The neotype (MNHN) is characterized by the following features: the pedicle is relatively long (L > D) and the burr is well-developed, with a circular cross-section. The antler beam becomes compressed from the sides above the burr, and the first tine is situated rather high above it. A well-expressed longitudinal groove is present on the lateral side of the beam between the first and second ramifications. Additionally, the anteromedial side of the beam bears a longitudinal groove-like depression, resulting in a pyriform cross-section in this part of the antler. The distance between the second and third ramifications is significantly longer than the distance between the first and second. The antler beam becomes compressed above the second ramification, forming a flattened part that terminates in the distal fork. The plane of the flattened portion of the beam is often perpendicular to the plane of the second ramification, although this character may be variable.

The right shed antler Nr. 211214 (PMUL) that has been identified as a type of *C. issiodorensis* exhibits the following morphological characteristics: a basal tine that is short and compressed from the sides, and a beam cross-section that is pyriform in shape. The antler Nr. 211214 from Lyon is a perfect match to figure 2 on pl. 1 in Croizer and Jobert's (1828) publication. Its measurements are highly comparable to those of the neotype of *C. perrieri*.

The measurements of the right astragalus Nr. 211205 (Croizet and Jobert, 1828: fig. 14, Pl. 2; L max = 60.1 mm, DLM dist = 37.8 mm) are very similar to the mean values of perrieri-ardei sample from Etouaires, as described in Heintz's (1970) study.

The deposits of Perrier-Eouaires have yielded the remains of two cervid forms of similar body size, one of which is *Praeelaphus perrieri*. The main challenge in studying the sample is its mixed character, as postcranial bones and lower mandibles are not directly associated with antlers and cannot be distinguished based on measurements and gross morphology alone. Heintz (1970) identified upper molars lacking a lingual cingulum as belonging to *P. perrieri*. Lower mandibles and postcranial bones of *P. perrieri* are practically indistinguishable from the remains of *Rucervus* (*Arvernoceros*) *ardei* from the same locality. All lower mandibles from Perrier are characterized by a relatively long premolar series, with the premolar/molar ratio of the mixed sample varying between 64.3% and 70.8%. Nonetheless, the lower cheek teeth series of the *perrieri-ardei* sample form two poorly distinguished clusters with somewhat shorter and comparatively longer premolar series. It is possible that the mandibles from Perrier-Etouaires with relatively shorter premolars belong to *P. perrieri*, while the mandibles with relatively longer premolar series belong to *Rucervus* (*Arvernoceros*) *ardei*, if we take the sample of *P. warthae* as a reference.

Distribution. Late Pliocene of Western Europe (France, England, Spain).

Praeelaphus lyra (Azzaroli, 1992)

Synonymy:

1972 *Cervus* (*Axis*) *cf. perrieri* (Croizet and Jobert): David and Shushpanov, p. 7, fig. 1.
1992 *Pseudodama lyra* sp. nov.: Azzaroli, p. 6, fig. 2, pl. 1, fig. 1 a-c.
1995 *Cervus rhenanus* (Dubois): de Vos et al., p. 112.
2000 *Axis nestii* (Azzaroli): Mazzini et al., p. 247.
2002 *Axis lyra* (Azzaroli): Di Stefano and Petronio: p. 319, fig. 7.
2006 *Cervus nestii* (Azzaroli) : Croitor, p. 91, fig. 1A.
2009 "*Cervus*" *lyra* (Azzaroli): Croitor and Stefaniak: p. 27.

Nomenclatural acts. The species was originally placed in the genus *Pseudodama* by Azzaroli (1992). *Pseudodama lyra* is based on well-preserved complete antlers attached to the frontal part of the skull from the Early Villafranchian of Ponte a Elsa (Lower Valdarno, Tuscany). However, the validity of this species has been questioned due to the superficial original description and unclear diagnosis. Azzaroli (1992) described *P. lyra* as differing from other species of *Pseudodama* in the curvature of the antler beam and the primordial bifurcation on the distal end of the antler. De Vos et al. (1995) included *P. lyra* in the synonymy of *Cervus* (s.l.) *rhenanus*, as the Italian species showed only minor morphological differences from *C. rhenanus*. Croitor (2006b) recognized a juvenile character of the asymmetric primordial branching of the distal part of the antler in *Pseudodama lyra* and included it in the synonymy of *Cervus nestii* (Azzaroli, 1947), while *Pseudodama*, based on *Dama nestii nestii* Azzaroli, 1947, was considered a junior synonym of *Cervus*. However, a further study of the specimen from Ponte a Elsa revealed its morphological similarity to *Praeelaphus perrieri*. Despite the great similarity between *Pseudodama lyra* and *P. perrieri*, I prefer to retain the species name *lyra* until a comprehensive comparative study is carried out.

Diagnosis: The first tine is positioned above the burr, and the ramification of the antler is acute. The beam of the antler has an irregular ovoid or pyriform transverse section, with shallow longitudinal grooves present on the medial and lateral sides. The antler segment between the first and second tines is relatively long compared to the distal segment, resulting in the middle tine being situated high. The second segment of the antler beam is short and flattened in the anteroposterior direction, with flattened extensions present in the area of ramifications. The surface of the antler is smooth, and the pedicles are compressed anteroposteriorly.

Holotype: the antlered frontlet IGF1934v (MGUF) of a young individual (Azzaroli, 1992: pl. 1, fig. 1).

Locus typicus: Ponte a Elsa, Lower Valdarno, Tuscany (Italy).

Stratum typicum: Triversa faunal unit (Pliocene, MN16, ca. 3.2 Ma: Gliozzi et al., 1997)

Description. The holotype IGF1934v consists of a complete pair of antlers with pedicels and frontal bones. The first tine arises high above the burr and forms an angle of 60° with the beam. It is thin, cone-shaped, slightly curved, and deviates slightly to the side. The angle of divergence between the first segments of the antler beams is 100°. The first segment of the antler is rather long and cylindrical. The cross-section of the antler beam between the first and second tines is irregular, similar to *Praeelaphus perrieri*, and the antler surface is relatively smooth. The distal portion of the beam above the second tine is short, curved inward, and flattened in the anteroposterior direction. The right antler terminates in a sharp point, while the left antler ends in two small prongs oriented in a frontal plane. The length of the right and left antlers is 73 cm and 78 cm, respectively. The pedicles are moderately long and flattened anteroposteriorly. The breadth of the skull behind the pedicels is 108.0 mm.

The asymmetry of the distal portions of the antlers from Ponte a Elsa suggests that this character may be unstable, and it is possible that full-size antlers of this species have four tines.

Additional material of this species has been found in the Pliocene of Moldova. The basal fragment of the antler attached to the pedicle "Luceşti-II-89" (IZK) shows a high position of the first tine, which springs off 79.4 cm from the burr (Croitor and Stefaniak, 2009: fig. 22). The first tine is rather long (165 mm) and has a circular transverse section. The basal ramification is at an angle of 70º. The basal segment of the antler beam is somewhat compressed lateromedially, and the antler measurements above the burr are 25.5 × 27.8 mm. The shape of the antler cross-section below the first ramification is an irregular trapezoid. The beam slightly deviates backwards from the first bifurcation, and the antler surface is rather smooth. The pedicle is moderately long and somewhat compressed anteroposteriorly, with a length of 27.0 mm. Several characteristics, such as the trapezoidal cross-section of the basal segment, the regular circular transverse section of the basal tine, the rather long compressed anteroposteriorly pedicle, the smooth antler surface, the angle of ramification, and the strong lateral compression of the antler in the area of ramification, suggest a close relationship between the antler from Luceşti and the type specimen of *Praeelaphus lyra* (Azzaroli, 1992) from Ponte a Elsa.

There is another specimen from the Late Ruscinian of Moldova that is similar to the previous antler. This is a basal fragment of a left shed antler (Nr. V-7/13-17, IZK) from Cociulia, originally identified as *Cervus* (*Axis*) cf. *perrieri* (David and Shushpanov, 1972: fig. 1). The antler from Cociulia is slightly smaller and belongs to a juvenile individual. The basal segment of the antler is compressed laterally, with two longitudinal ribs running from the base of the first tine to the burr on the anterior side of the antler. The cross-section of the antler above the burr is trapezoidal, as in the specimen from Luceşti. The anteroposterior diameter of the antler above the burr measures 23.8 mm, while the lateromedial diameter measures 23.9 mm. The basal tine is cone-shaped, measuring 76 mm in length. The height of the antler ramification is 49.3 mm, with an acute angle of ramification (35°). The antler surface is smooth.

The antlers of *P. lyra* resemble those of *P. perrieri* but are more slender. The holotype of *P. lyra* appears to belong to a young individual and did not achieve full development, as the antlers are characterized by flattening of the distal beam segment, specific to *P. perrieri* and *P. warthae*, but the distal bifurcation is not yet developed. *P. lyra* can be clearly distinguished from *M. rhenanus* by the irregular or pyriform shape of the cross-section of the antler beam segment between the first and second tines, and by the anteroposterior flattening of the distal portion of the antler.

Distribution: Pliocene; Late Ruscinian (MN15), Moldova – Early Villafranchian (MN16), Italy.

Praeelaphus warthae (Czyżewska, 1968)

Synonymy:

1959 *Cervus* (*Rusa*) sp.: Czyżewska, p. 132, figs. 2-3.
1968 *Cervus warthae* sp. nov. (partim.): Czyżewska, p. 573, pls. VI-VIII.
1977 *Cervus philisi* (Schaub): Alekseeva, p. 129, fig. 25.
1990 *Cervus* (*Rusa*) *warthae* Czyżewska, 1968: Vislobokova, p. 154.
2001 *Pseudodama warthae* (Czyżewska, 1968): Stefaniak, p. 19, figs. 23-39, 60, 69.
2012 *Praeelaphus warthae* (Czyżewska, 1968): Croitor, p. 223.

Nomenclatural acts. The species was originally described based on fragmentary material from the breccia of Węże-1 Cave in Poland. Due to the poor preservation of the antlers, the systematic position of this species could not be determined, although many authors suggested that *Cervus warthae* showed some affinities with modern *Rusa* (Czyżewska, 1968; Vislobokova, 1990). However, a revision of the antler material revealed a close affinity between the deer from Węże-1 and *Praeelaphus warthae* (Croitor and Stefaniak, 2009).

Diagnosis: This species can be distinguished from the genotype species by its smaller size and four-pointed antlers, with the basal tine located close to the burr. The proximal part of the antler beam has a pyriform cross-section, and the antler ramifications form flattened connections between the antler beam and the middle and distal tines. Above the second tine, the antler beam becomes compressed anteroposteriorly. The frontal bones are concave before the pedicles, and the orbitofrontal part of the skull is short, with the anterior edge of the orbit situated above M^3. Upper molars feature a protoconal fold (bifurcated protocone) and a hypoconal spur, and the entostyle is weak or moderately developed. The cingulum is not developed in the upper molars, and the lingual walls of P^2 and P^3 are cleft. The lower tooth series is relatively long, and P_4 is not molarized and is considered primitive.

Holotype: the skull Nr. 1 (IZW, Fig. A.17) of a young adult male with full permanent dentition that shows some wear. The skull preserved only a part of the braincase, the frontal bones with destroyed pedicles and the right maxilla with P^3-M^3.

Locus typicus: Węże-1, Poland.

Stratum typicum: Pliocene breccia of Węże-1 Cave

Description. *P. warthae* is a medium-sized deer, with a mean estimated body mass of 120 kg and a maximum predicted body mass of 145 kg. The parietal bones are slightly convex and the orbitofrontal part of the skull is short, with the anterior edge of the orbit situated above M^2/M^3. The pedicles slope backwards, and the frontal profile is convex between the pedicle bases before becoming depressed between the orbits. The frontal bones are somewhat depressed in the area between the frontal suture, the pedicle base, and the orbit, but slightly swollen in their anterior part where they join the nasal bones. The breadth of the frontal bone, measured from the frontal contraction in front of the pedicles to the frontal suture, is 53 mm. The elongated supraorbital channel is located approximately 25 mm medially to the frontal edge in the area of forehead contraction and 26 mm from the frontal suture. Additional cranial characteristics of *P. warthae* from Węże-1 (IZW) include a swollen anterior part of the frontal bones, large and deep preorbital fossae, a broad and bell-shaped basioccipital bone, and round, smooth bullae tympani devoid of the bony thorn, which is characteristic of *C. elaphus* (Croitor and Stefaniak, 2009).

The skull fragment Nr. 346 comprises the left part of the occipital bone and almost the entire basioccipital bone. The bell-shaped basioccipital bone is extended in the area of the pharyngeal tuberosities, with a breadth of 25.4 mm at this point. Additional measurements from skull fragment Nr. 362 (Czyżewska, 1959: pl. III, fig. 1) include a bulla tympani diameter of 15.5 mm, a breadth of 29.0 mm at the pharyngeal tuberosities, an occiput breadth of 89.0 mm, and an occiput height of 68.5 mm.

The upper molars of skull Nr. 1 (IZW) feature a small entostyle, a hypoconal spur, a small enamel fold on the posterior wing of the protocone, and an additional small interior enamel fold on the anterior wing of the protocone. The upper third premolar (P^3) displays a cleft lingual wall and hypocone and protocone separated from each other. The hypocone is supplemented with an internal enamel fold. The lingual wall of the upper fourth premolar (P^4) is not cleft; its hypocone is supplemented with an internal bifurcated enamel fold. The lower fourth premolar (P_4) is primitive, with separated parastylid and paraconid. The metaconid is extended anteroposteriorly but does not connect with the paraconid and entoconid. The lower molars bear ectostylids.

The antlers of *P. warthae* had four tines when fully grown. Basal fragment Nr. 312 is from a robust, heavy right antler that was attached to a pedicle, which is now broken off. The first tine is directed anteriorly and is situated at a small distance from the burr. The antler beam is set obliquely above the basal ramification, forming an obtuse angle of 125 degrees with the basal tine. The antler base has a circular shape, and the beam is compressed in the lateromedial direction above the basal ramification. The basal tine has a pyriform transverse section in the broken part. The antler surface has deep longitudinal furrows and ridges, with pearlings covering its medial side. The diameter of the pedicle below the burr is 41.3 mm, the anteroposterior diameter of the antler above the burr is 54.1 mm, and the basal ramification height is 58.2 mm. The vertical diameter of the antler beam above the ramification is about 45 mm, and the horizontal diameter is 31.5 mm. The vertical diameter of the basal tine near the breakage is 37.2 mm, and the horizontal diameter is 29.6 mm.

Fragment of antler tine Nr. 323 most probably belongs to the previous specimen. The gently curved tine is sculptured by furrows and ridges. The antler beam is presented by several damaged fragments (Nr. 313 and Nr. 314), and its transverse section is pyriform. Antler fragment Nr. 318 represents a 70-mm-long portion of the antler just below a ramification. The transverse diameter of the beam is 26.1 mm, and the antler extends anteroposteriorly toward the ramification. The antler surface between the beam and the tine axis is depressed, and the angle between the axis of the beam and the tine makes about 15 degrees. The antler surface is rather smooth and ornamented by shallow, small longitudinal furrows.

Fragment Nr. 316 represents a distal portion of an antler immediately below a bifurcation. The fragment is about 69 mm long and represents the main antler axis and the base of the additional axis that springs off at an angle of 15 degrees. One side of the fragment is more or less flat, and the opposite side is concave between the axis of the beam and the ramification. The antler fragment is slightly twisted clockwise towards the flat side distally. The transversal diameter of the main antler stock is 29 mm, and the transversal measurement of the additional axis is 16 mm. The antler surface is rather smooth, as in the previous specimen.

The fragment of the distal portion of the antler (no number) is quite interesting. It comprises a tine and a part of an antler beam above the second ramification. The antler beam is rather flat, suggesting a remarcable flattening in the anteroposterior direction. The tine is cylindrical, slightly curved, and forms an acute angle of approximately 40 degrees with the beam. The tine's diameter varies from 23.4 mm near its base to 17 mm in its distal portion, and the preserved part of the tine is 180 mm long. The surface of the specimen is grooved with deep longitudinal furrows.

The antler beam segment between the first and second tine is cylindrical, with a circular or ovoid cross-section. The antler segment above the second tine is flattened with the plane of flattening oriented in the frontal plane, suggesting that this flattening terminates in a distal fork. The lower tooth series of *P. warthae* is relatively smaller than the sample of *perrieri-ardei* from Perrier-Etouaires. Additionally, the lower premolar series of *P. warthae* is longer than in modern *Cervus elaphus* and *Eucladoceros ctenoides* from Sénèze, indicating a more primitive condition of this character.

Distribution. Late Ruscinian (MN15), Poland.

Praeelaphhus australorientalis Croitor, 2017

Diagnosis: This is a medium-sized deer similar in body size to modern fallow deer *Dama dama*. The males have a rather long braincase, with the bregma-opisthocranion distance longer than the braincase breadth behind pedicles. The males also have comparatively narrow frontal bones, with the braincase breadth behind pedicles measuring about 80% of the frontal constriction before the pedicles. The pedicles are robust and moderately long, with the length of the pedicle in mature males reaching about 2/3 of the pedicle lateromedial diameter. The small bullae tympani are characterized by an irregular shape and a short auditory tube. The antlers are robust and have four tines. The first and second tines are inserted on the anterior side of the antler beam. The first tine is situated very high above the burr, with the height of the first ramification exceeding more than two times the diameter of the basal part of the antler beam. The antler segment between the first and second tines is comparatively short, shorter than the height of the first ramification. The distance between the second and distalmost third ramifications is three times longer than the distance between the first and second ramifications. The basal segment of the antler beam, below the first ramification, is regularly circular. The beam segment between the first and second ramifications has a longitudinal keel on the anterior side. The antler beam between the second and third ramifications is significantly flattened, oriented in the parasagittal plane and terminates with a distal bifurcation. The anterior tine of the distal bifurcation is stronger and represents a continuation of the antler beam axis.

. **Holotype**: the antlered skull OF-24995 (NMENH) with the main part of the right antler, the basal part of the left antler, and the distal detached fragment of the left antler (Fig. A.18).

Locus typicus: Velikoploskoe Village (= Velikoe Ploskoe), Odessa Region (Ukraine).

Stratum typicum: gravel lenses of the Kuchurgan fluviatile deposits.

Description. The antlered braincase OF-24995 belongs to a medium-sized cervid similar in size to modern fallow deer. However, the greater part of the left antler is destroyed, and only its proximal portion (150 mm of total length) is preserved. There is also a distal fragment of the left antler that belongs to the same individual and represents a part of the antler beam between the second tine and the distal bifurcation. The right antler is better preserved, except for its first tine and the distal portion. The antlers are relatively robust and lyre-shaped with well-developed and strong burrs. The cross-sectional shape of the antler base is slightly compressed in the anteroposterior direction, and the surface is densely covered with sharp longitudinal ribs and furrows. The median and posterior sides of the proximal portion of the antlers are sculptured with graininess and tubercles.

In the better-preserved right antler, the first tine is situated very high relative to the burr, with the height of the first ramification measuring about 105 mm. The second tine is inserted on the anterior side of the beam at a short distance from the first tine, with the length of the antler segment between the first and the second ramifications measuring 78.0 mm. The second tine is cone-shaped and rather short, with a circular transverse section. Its length is 61.0 mm, and the transverse diameter at the base is 18.7 mm. The angle of the second ramification measures 35°.

The distal portion of the left antler is a beam segment between the second and the third ramification. The cross-section of the proximal end of the fragment is ovoid with a sharpened posterior side (DAP = 34.4 mm; DLM = 32.7 mm). The antler beam extends anteroposteriorly above the second ramification and becomes fairly flattened toward the third ramification. The thickness of the antler beam in the area of the distal bifurcation is 25.2 mm. The anterior tine of distal bifurcation is more robust (its transversal diameter at the level of bifurcation attains 24.8 mm) and represents a continuation of the beam axis. The posterior tine is thinner (its transversal measurement at the same level amounts to 20.1 mm) and slightly deviates posteriorly from the axis of the main antler beam. The median side of the distal antler portion is rather flat, while the lateral side is convex. The total length of the distal fragment of the left antler attains 235 mm, while the length of the left antler beam segment between the second and the third ramification amounts to 233 mm. The length of the right antler segment between the second and the third ramifications exceeds 200 mm.

The pedicles have a moderately long and circular cross-section and are slightly compressed in the anteroposterior direction, with an angle of divergence formed by pedicle axes of 40°. The frontal bones are narrow and slightly depressed between the frontal suture and their lateral margins. The roof of the braincase is slightly convex, and the lambdoid suture between the temporal and occipital bones is trapezoidal. The basioccipital is pentagonal-shaped due to a moderate extension of the pharyngeal tuberosities. The foramen ovale is not particularly large and is oval in shape, with a maximal diameter of 4.6 mm, set obliquely to the sagittal plane, as seen in advanced Old World deer (Vislobokova, 1990).

The bullae tympani are quite small and have an irregular shape, with anteroposterior measurements of sin 12.9 mm and dx 13.2 mm, without any apical thorn or spike. The shape of the bullae tympani is similar to that of *Axis axis*, as reported by Pocock (1943). The external auditory tube is rather short, with a measurement from the auditory orifice to the inner anterior edge of the bulla tympani of 30.4 mm (dx) and 27.5 mm (sin), which is about 25% shorter than that of the modern primitive Cervini *Axis axis* and *Hyelaphus porcinus*, according to the data provided by Pocock (1943). Although both tympanic bullae are present, the left os temporale is damaged, making it possible to directly observe the post-glenoid foramen morphology. The post-glenoid foramen is closed from the medial side by the bony bridge of squamosal bone, which distinguishes plesiometacarpal cervids from telemetacarpal cervids (Bouvrain et al., 1989).

The index of relative braincase length (the bregma-opisthocranion length to braincase breadth ratio) of *P. australorientalis* is 107.9%, which is similar to some fossil and recent cervids (*Metacervocerus rhenanus*, *Cervus nestii*, *C. elaphus*) and modern *Muntiacus muntjak* and *M. reevesi*. The braincase of *P. australorientalis* is relatively shorter and broader than in *A. axis*, *Rucervus duvaucelii*, *Panolia eldii*, and the mean values of modern *Dama dama* (Croitor, 2017).

The bregma-opisthocranion length to braincase breadth ratio varies from 92.4% to 108.7% (n = 8) in modern fallow deer males, with a mean value of 98.2%. In females (n = 5), the ratio ranges from 91.9% to 101.7%, with mean values of 97.6%, which are practically equal to the index obtained for males. The small sample (n = 4) of *A. axis* crania suggests a braincase shape index similar to *Dama dama*, with a variation range from 94.0% to 101.5% and a mean value of 97.6%. *P. australorientalis* is characterized by a frontal bone to overall braincase breadth ratio of 80.2%, which is close to *Elaphurus davidianus* (80.3%, n = 1), *C. nippon* (80.1%, n = 1), *D. dama* (74.1% to 87.6%, n = 8), and *M. rhenanus* (75.4% to 88.9%, n = 4). However, the frontal breadth in *P. warthae* is relatively larger than in *P. australorientalis*, with a braincase breadth reaching only 73.7% of the frontal breadth in a young male individual (measured from the type specimen of *P. warthae* Nr. 1 from Weze-1).

In small/medium-sized cervids, the shape of the occiput (the ratio between occiput height and occiput width) varies insignificantly and is similar in cervines with various relative antler sizes and weight. The index of occiput shape amounts to 63.8% in males of *D. dama* with relatively large palmed antlers, which is close to the index obtained for *H. porcinus* with small three-pointed antlers (61.4%, n = 3). The index of occiput shape in *P. australorientalis* (64.8%) falls within the variation of both *D. dama* and *H. porcinus* and is significantly lower than in *P. warthae* from Weze-1 (77.0%; the cranial fragment Nr. 362). Therefore, the neurocranium of *P. australorientalis* is comparatively short and broad and is similar to the modern *Cervus*, *Muntiacus*, and Late Villafranchian *Metacervocerus*. The frontal bones are relatively narrow, as in the majority of small/medium-sized and larger cervids.

Specimen Nr. 231, a proximal antler fragment from the Early Pliocene of Berești (Romania), is also identified as belonging to *P. australorientalis* and is curated at the Institute of Speleology of Bucharest. The specimen measures 69.0 mm in length above the burr and does not exhibit any indication of the first ramification at this height. The pedicle is moderately long and somewhat anteroposteriorly compressed. The burr has an irregular shape, measuring LDM = 51.7 mm and DAP = 43.6 mm. At the point of breakage, the antler has a mediolateral diameter of 41.5 mm and an anteroposterior diameter of 31.2 mm (Croitor, 2017).

Distribution. Early Pliocene, MN14 – beginning of MN15, Southeastern Europe (Ukraine, Moldova, Romania).

Praeelaphus sp. from Olivola

Synonymy:

1947 *Dama nestii nestii* ssp. nov.: Azzaroli, p. 52, fig. 1-7; p.55, fig. 4-1.
2012 *Praeelaphuus lyra* (Azzaroli, 1992): Croitor, p. 223, fig. 2.
2014 *Praeelaphus cf. lyra* (Azzaroli, 1992): Croitor, p. 128, fig. 10.

Comments. An antlered braincase IGF1378 of *Praeelaphus* sp. from Olivola (Fig. A.19) represents one of the last members of the genus *Praeelaphus* found in the Late Villafranchian of Tuscany (Italy). Initially described by Azzaroli (1947) as *Dama nestii nestii*, the specimen with the left antler belongs to a mature male individual (sutures of the braincase are obliterated) and shows characteristic antler morphology of *Praeelaphus*. The braincase is slightly flexed and relatively short, similar to *P. australorientalis* (the ratio of bregma-opisthocranion length to neurocranium breadth amounts to 107.9%). The parietal bones are slightly convex, the pedicles are moderately long, slightly compressed anteroposteriorly, and somewhat inclined backward. The basioccipital is bell-shaped and broadened in the pharyngeal tuberosities, as in *P. australorientalis* and *P. warthae*. The preserved left bulla tympani is moderately large, smooth, and rounded, as in *P. warthae*.

While the first tine is not preserved, it appears that the first ramification is situated relatively high above the burr, though not as high as in *P. australorientalis*. The cross-section of the antler base is circular, but the antler forms a specific anteroposterior extension below the first ramification. The antler beam is cylindrical above the first ramification and extends anteroposteriorly below the second ramification, as in *P. lyra*. The side surfaces of the antler are concave in the area of the second ramification. The second tine is somewhat compressed anteroposteriorly, set perpendicular to the flattened portion of the antler beam, and located at a long distance from the first tine, much longer than in *P. australorientalis*. The antler beam above the second tine is strongly compressed in the anteroposterior direction and gradually becomes broadened distally. The distalmost part of the antler is not preserved. The perpendicular orientation of the second antler ramification to the plane of the flattened distal part of the beam is a variable character in the sample from Olivola.

Additionally, the fragment of the right hemimandible IGF1394 from Olivola with molarized P_4 could be assigned to this cervid form.

Praeelaphus from Olivola is most likely a distinct species, although a detailed study is needed to confirm this, as the Olivola fauna also includes another small cervid, *Cervus nestii* (Croitor, 2014). The small-sized *Praeelaphus* persisted on the Italian peninsula until the "wolf event" faunal turnover, becoming extinct just before the dispersal of the first primitive fallow deer, *Dama eurygonos*, with simple four-tined antlers in the Tasso F.U. It appears that the presence of *Praeelaphus* in the Early Pleistocene of the Italian Peninsula is indicative of a biogeographic refugial character. Additionally, *Praeelaphus* may have also survived in the Transcaucasian refugium; some cervid remains from the Early Pleistocene fauna of Dmanisi (Georgia) may be attributed to this genus (Croitor, 2017).

Distribution. Early Pleistocene, Late Villafranchian, ca. 1.8 Ma, Italy.

Praeelaphus messinae (Pohlig, 1909)

Synonymy:

1909 *Cervus* (*Megaceros*) *messinae* sp. nov.: Pohlig, p. 251, fig. 1.

Diagnosis. A muntjac-sized deer with thin three-pointed antlers. The first tine is situated above the burr at a distance exceeding the diameter of the antler base. The distal bifurcation is composed of the strong and long posterior tine that is a continuation of the main axis of the antler, and the smaller tine inserted on the anterior side of the beam. The antler forms a remarkable flattening in the area of the second ramification. The antler is characterized by the presence of two well-expressed longitudinal groves each of which ranges along the antler axis from the lateral and medial sides. The cross-section of the beam between the basal and second tines is pyriform. The antler surface is pearled.

Holotype. The left antler with pedicle figured by Poglig (1909).

Locus typicus. Puntali Cave near Carini, Sicily.

Stratum typicum. The "Norfolk interglacial" layer of the Puntali Cave (Pohlig, 1909).

Description. The small deer discovered in the Puntali Cave is characterized by thin, palmated antlers with at least three tines, including the basal tine, the second tine which is likely the homology of the middle (trez) tine, and the distal, strongest tine which represents the continuation of the main beam (see Fig. A.20). The preserved length of the antler (excluding the distal small part that is missing) measures over 23 cm, while the diameter of the antler base is approximately 15 mm (measurements calculated from the figures provided by Pohlig in 1909). The antler is distinguished by the rather high position of the small basal tine (about 3 cm from the burr), a robust second tine located on the anterior side of the beam, and a palmation-like extension between the main beam and the second tine. The antler surface exhibits a pearled appearance.

According to Pohlig (1909), the small deer from the Puntali Cave represents a dwarfed insular form of the giant deer *Megaloceros giganteus*. The high position of the basal tine and the pearled antler surface exclude any possible evolutionary relationship between *M. giganteus* and *C. messinae*. The Sicilian dwarfed deer shares specific antler characteristics with *P. perrieri*, such as longitudinal shallow grooves and a remarkable flattening in the area of the second ramification. Pohlig (1909) interpreted this feature as a homology of the giant deer's palmation.

Distribution: the Middle Pleistocene, Sicily. The dwarfed deer from the Puntali Cave most probably is the last representative of *Praeelaphus* that survived into the Middle Pleistocene in the insular refugium.

Genus *Rucervus* Hodgson, 1838

The emended diagnosis of Hodgson's (1838) original description: the body size ranges from medium to very large; the antlers are of moderate size, with a basal anterior tine and distal crown tines that are inserted on the posterior side of the beam. The crown tines are frequently dichotomously branched, while the basal tine is often supplemented with an accessory prong or is branched. No middle tine is present. The braincase is moderately flexed, and the parietal bones are not convex. The basioccipitale is bell-shaped and broadened in the pharyngeal tubercles. Both sexes possess small upper canines.

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

Comments. In Hodgson's (1838) original diagnosis of *Cervus* (*Rucervus*), he stated that upper canines were only present in males. Pocock (1943) later confirmed this statement, but he had only been able to check this character in a single female skull of *Rucervus duvaucelii* that had been studied by Hodgson. However, according to craniological material stored in the MNHN, upper canines are present in both sexes of *R. duvaucelii*.

The genus *Arvernoceros* Heintz, 1970 was defined based on *Cervus ardei* Croizet et Jobert, 1828 from the Late Pliocene (Early Villafranchian) of Perrier-Etouaires (France). This definition generally corresponds to the diagnosis of *Rucervus*, and therefore *Arvernoceros* is considered a junior synonym of the latter, or at most, it could be regarded as a subgenus of *Rucervus*, as proposed in the present study.

Subgenus *Arvernoceros* Heintz, 1970

Diagnosis. The first tine is situated comparatively higher above the burr; the height of the first ramification is no less than twice the basal diameter of the antler; the crown part of the antler is relatively shorter (about 1/3 of the antler beam length or less) and often is palmated. P_4 is not molarized and maintains a primitive morphology. The crown of P_2 is always shorter than the crowns of P_3 and P_4.

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

Distribution. Early Pliocene–Early Pleistocene, Western Eurasia.

Rucervus (*Arvernoceros*) *ardei* (Croizet and Jobert, 1828)

Synonymy:

1828 Second sous-genre: Croizet and Jobert, pl. 1, fig. 1, pl. 2, figs. 2-3, pl. 3, fig. 2.
1853 *Cervus ardeus* Croizet et Jobert, 1828: Pomel, p. 108.
1878 *Cervus cylindroceros* sp. nov.: Dawkins, p. 412, fig. 11.
1884 *Cervus* (*Polycladus*) *ardeus* Croizet: Deperet, pl. V, fig. 1.
1884 *Cervus* (*Axis*) *borbonicus* Deperet: Deperet, p. 260, pl. VI, figs. 1, 2.
1970 *Arvernoceros ardei* (Croizet et Jobert, 1828): Heintz, p. 241, fig. 295.
2018 *Rucervus ardei* Croizet et Jobert, 1828): Croitor, p. 4.

Nomenclatural acts. The cranial and antler remains of this species appear on plates 1 (fig. 1), 2 (figs. 2-3), and 3 (fig. 2) entitled "Cerfs fossils de la montagne de Perrier (Second sous-genre)" in "Recherches sur les ossementes fossils" of Croizet and Jobert (1828). Pomel (1853) gave a definition of *Cervus ardeus* based on the figured by Croizet and Jobert (1828) specimens and mentioned a fairly complete antler with a small distal palmation that could be close to *C. ardeus* and was not figured before. This specimen appeared much later in figure 1 of plate V published by Deperet (1884). Heintz (1970) selected the antler similar to the figured by Deperet (1884) specimen as a neotype and this nomenclatural act was never contested afterwards.

Diagnosis: Fontal bones are flat, pedicles are comparatively long, robust, and weakly divergent, slopped backwards, and almost lie on the plane of the frontal bones. The space between pedicles is comparatively small. The braincase is relatively short and broad: the distance between the bregma and opisthocranion anatomical points significantly exceeds the braincase breadth behind pedicles. The first tine is situated high above the burr, flattened and supplemented with an additional prong. The antler beam is bent backwards in the area of the first ramification. The cross-section of its proximal part is regularly circular. The distal third of the antler becomes laterally compressed and terminates with three tines. The antler surface is smooth.

Neotype: the almost complete left antler PET5095 (MNHN) missing burr part.

Locus typicus: Les Etouaires, Puy-de-Dôme, France.

Stratum typicum: alluvial layers of Etouaires, Lower Villafranchian.

Description. *Rucervus (Arvernoceros) ardei* is a large deer, weighing approximately 180 kg. This species exhibits a combination of primitive and advanced features. Among the primitive characteristics should be mentioned long, backward-sloping parallel pedicles, simple antlers that correspond to the three-pointed stage of antler evolution, and relatively primitive dentition with a long premolar series and simple P_4. The advanced features include a large body size, short and broad braincase, and distal antler palmation in mature males. The antler structure is generally simple, with a high first basal tine that may be slightly flattened and accompanied by a small accessory prong. The antler beam terminates in a small distal fork, which may extend into a small terminal palmation with three tines in mature specimens, resulting in a total number of four tines.

The neotype antler of *R.* (*Arvernoceros*) *ardei* has a regularly circular cross-section of the beam, but it becomes compressed and bends towards the posterior at the area of the first ramification. The first tine is flattened and has an accessory prong. The diameter at the middle of the tine is 37.5 mm, with a minimum diameter of 21.0 mm. The maximum diameter of the first tine runs obliquely upwards from the median side to the lateral one. The beam regains its cylinder shape above the first ramification, with a DLM of 33.0 mm and DAP of 32.5 mm. The upper third of the antler gradually becomes compressed and extends into a small palmation with three tines. The distal palmation of the type specimen has three tines pointing forwards, which may not be typical. The anterior tine of the palmated part of the antler may be interpreted as the apical part of the beam, while the other two tines are crown tines inserted on the posterior side of the beam. The distal fragment of antler PET1024 (NMNH) from Perrier suggests that the palmation was bilobed, with two prongs on the preserved posterior lobe of palmation. This specimen is better described as a palmation lobe terminated with two tines and separated from the anterior part of the palmation by a deep incision. The breadth of this part of the palmation is 69.0 mm, and the distance between the palmation incision and the distal bifurcation of the posterior palmation lobe is 99 mm. The thickness of the antler fragment varies between 20.6 and 18.0 mm.

The fragment of frontal bone PET1020 (Heintz, 1970: p. 128, fig. 306, pl. XX, fig. 4a, b) that includes the proximal part of the antler exhibits a strongly compressed first tine at its proximal end (DAP: 51.0 mm, DLM: 28.0 mm). The accessory prong is situated behind and medially to the first tine, with the apical part broken off. The remaining length of the accessory prong is 48 mm (Tab. A.6).

Unfortunately, well-preserved cranial material of *R. ardei* is lacking. The available skull fragments provide some unique characteristics of the braincase and pedicles. The neurocranium PET1053 (Heintz, 1970: p. 129, fig. 310) exhibits convex frontal bones before pedicles and strong pedicles with a circular cross-section and a relatively small distance between their bases. The angle between pedicles is 50°, while the parietal bones are slightly concave. The basioccipitale is slightly broadened at pharyngeal tuberosities, bell-shaped. The preserved proximal parts of antlers deviate anteriorly from the pedicle axis, and the antlers become compressed on the sides in the area of the first ramification.

The cranial fragment PET1052 (Heintz, 1970: p. 128, fig. 309, pl. XX, fig. 1a, b) is characterized by long, strong, and cylinder-shaped pedicles. The profile of the frontal bones is convex between the pedicles and concave above the posterior parts of the orbits. The pedicles are sloped backwards, almost parallel, and lie on the plane of frontal bones. The first tine is situated very high above the burr (Tab. A.6). The antlers are strongly compressed in the area of the first ramification. The right antler maintains a small accessory prong in the area of the first ramification, situated somewhat medially on the antler (as in *Eucladoceros*). The antler beam is directed backwards from the first ramification. The beam of the left antler is broken at 20 cm from the ramification, and its measurements at this point are 40.5 mm (DAP) and 31.5 mm (DLM).

Heintz (1970) attributed upper cheek teeth with cingula to *R.* (*Arvernoceros*) *ardei*, assuming that the flattened basal tine and upper molars with cingula prove its direct phyletic relationship with *Megaloceros giganteus*. Heintz (1970) could not associate the antlers from Perrier-Etouaires (France) with lower mandibles since the sample of fossils represents a mixture of remains of two equally sized cervids *R. ardei* and *Praeelaphus perrieri*. Nonetheless, as already suggested, *R. ardei* is characterized by a simple, unmolarized P_4 and a relatively long series of lower premolars.

The shed right antler from the Villafranchian deposits of Slobozia Mare (Moldova) is quite small but shares with *R.* (*Arvernoceros*) *ardei* from the type locality the flattened shape of the first tine, the high position of the first ramification, and the cylinder-shaped beam (Fig. A.21). Unlike the antler from the type locality, the beam of the Moldavian antler is not turned backward from the first ramification. The antler from Slobozia Mare is very close to the antler variant described as "*Cervus cylindroceros*".

Distribution. *R*. (*Arvernoceros*) *ardei* was documented by Heintz (1970) at various Lower Villafranchian sites in France and Spain. The earliest evidence of *R*. (*Arvernoceros*) in Europe was found at Węże-1 (Poland) from the Late Ruscinian (Early Pliocene); this is a frontal part of the skull that is morphologically similar to the frontal shape of *R*. (*Arvernoceros*) *ardei* from Perrier-Etouaires (Croitor and Stefaniak, 2009). The shed antler from the Villafranchian deposits of Slobozia Mare (Moldova) expands the range of *R*. (*Arvernoceros*) *ardei* to southeastern Europe.

Rucervus (*Arvernoceros*) *radulescui* Croitor, 2018

Synonymy:

1977 *Cervus philisi* Schaub, 1941: Alekseeva, p. 129, fig. 25.
1990 *Eucladoceros sp*.: Radulesco and Samson, p. 227.
2005 *Eucladoceros ctenoides* (Nesti, 1841): Kostopoulos and Athanassiou, p. 182, fig. 3.
2008 *Arvernoceros sp*.: Titov, p. 104, tab. 46.
2009 *Arvernoceros sp*.: Croitor, p. 382, fig. 3, D.
2015 *Eucladoceros sp*.: Curran, p. 299.

Diagnosis. The body size is similar to that of modern European red deer. Antlers are thin and large, with a distal crown transformed into a small palmation divided into two lobes terminated with tines. The antler beam cross-section is oval. The basal tine is situated at a long distance from the burr: the basal ramification height exceeds 2–3 times the antler base diameter. The lower fourth premolar (P_4) is simple.

Differential diagnosis. The new species differs from *E. ctenoides* and *E. dicranios* in its antler structure. *R. radulescui* has up to three tines (which may be bifurcated) on the posterior side of the distal portion of the beam, forming the antler crown. In contrast, *Eucladoceros* has three to five crown tines inserted on the anterior side of the beam. Moreover, *R. radulescui* lacks the accessory prong situated somewhat medially in the area of the first ramification, which is present in *Eucladoceros*.

Compared to *Rucervus simplicidens*/*colberti* from the Siwalik fauna, *R. radulescui* has a relatively high position of the first ramification, a shorter crown segment of the antler, and a palmated distal portion of the antler. Furthermore, the new species differs from *R. ardei* (Croizet and Jobert, 1828) from the Late Pliocene of Perrier-Etouaires (France) in the absence of a small additional prong on the basal tine, the somewhat divergent pedicles, and the practically complete reduction of the lingual cingulum in the upper molars. *R. radulescui* has a pronouncedly oval cross-section of the beam, unlike both *R. ardei* and *R. simplicidens*/*colberti*.

R. radulescui is distinguished from *R. verestchagini* (David, 1992) from the Early Pleistocene of Salcia (Moldova) by its significantly smaller body size, the simple cylinder-shaped first tine (not flattened and trifurcated as in *R. verestchagini*), and the well-developed distal palmation.

Locus typicus. Valea Grăunceanului (=Grăunceanu, =Bugiulești, =Roșiile), western slope of the Dealul Viilor Hill, Tetoiu Area, Vâlcea County, Southern Romania.

Other sites. Salcia (Moldova), Morskaya Station, Liventsovka (Russia), Gerakarou (Greece).

Stratum typicum. Lower faunal horizon (T-1), Early Pleistocene, MN17-MQ1; correlated with the Tiglian C5 warm stage of the Netherlands and the fauna from Volakas in Greece (Croitor, 2018a)

Holotype. The shed antler with collection number "GR-965, c. 17, v. 690" (ISER) belongs to a young adult individual (Fig. A.22). The first (basal) tine is broken off, and the distal palmation is damaged, including the anterior lobe, which corresponds to the apical portion of the antler. The posterior lobe of palmation terminates into two tines, with the apical parts of those tines broken off. The preserved antler part has a total length of approximately 540 mm. The antler base is oval-shaped, with a DAP of 43.6 mm and a DLM of 36.6 mm. The antler circumference above the burr is 125 mm. The height of the first ramification is 106.2 mm and there is a specific sharp rib connecting the beam and the first tine in the area of ramification. The distance between the first ramification and the distal palmation measures approximately 290 mm. The beam is S-shaped, gently curved backwards above the first ramification, and then moderately bowed towards the anterior, gradually expanding into the distal palmation, which is slightly concave from the medial side. The breadth of the posterior lobe of palmation is 89.0 mm. The antler surface is smooth, without pearling, and the longitudinal ribs and furrows are moderately expressed. The beam cross-section is oval.

Rucervus (*Arvernoceros*) *verestchagini* David, 1992

Synonymy:

1992 *Arvernoceros verestchagini* sp. nov.: David, p. 67, fig. 1.
2018 *Rucervus* (*Arvernoceros*) *verestchagini* David, 1992: Croitor, p. 4, fig. 15e.
2019 *Arvernoceros verestchagini* David, 1992: Vislobokova et al., p. 597, fig. 1.

Diagnosis: the species is characterized by its very large size. The antler beam is cylindrical in its proximal part and laterally compressed in its distal third. The basal tine is positioned high above the burr and terminates in a small palmation with three prongs. The distal crown consists of a single tine that arises from the posterior side of the beam, resulting in a simple fork termination. The distal palmation is absent.

Holotype: the shed left antler from Salcia (IZC).

Locus typicus: Salcia Quarry, Moldova.

Stratum typicum: lower sand deposits of Salcia Quarry, Villafranchian.

Description. This species exhibits a large body size (similar to modern wapiti *Cervus canadensis*) and relatively simple antler morphology. The holotype antler shares a general bauplan with *R*. (*Arvernoceros*) *ardei*, but is notably larger (David, 1992). The antler circumference above the burr measures 277 mm, and the preserved length of the antler is approximately 1 meter, with the apical portion being destroyed. The proximal part of the antler beam is cylindrical in shape, with the first tine positioned high above the burr. This tine is robust and extends into a small palmation with three prongs that exhibit an inward curvature. The first tine likely exceeds 400 mm in length, and the breadth of the palmation at the base of the prongs is approximately 220 mm. The distance between the base of the first tine and the two upper prongs of the ramification is 300 mm, and the circumference of the narrowest part of the first tine is 205 mm. The antler beam is moderately curved backwards in the area of the first ramification before turning upright in the middle of the antler part above the first ramification, gradually becoming flattened. The circumference of the beam above the first ramification is 221 mm. The distal part of the antler does not form a palmation, but rather is flattened, ending with a simple distal bifurcation. The distance between the first and second ramifications is 715 mm. The DAP and DLM of the antler beam above the second ramification are 74.7 mm and 44.8 mm, respectively. It is unclear whether the destroyed distal part had another ramification or not.

Distribution. Early Pleistocene of Moldova (Salcia) and Ukraine (Crimea, Tavrida Cave) (Vislobokova et al., 2019).

Rucervus sp. from Venta Micena-2

Comments. Menendez (1987) described remains of a medium-sized deer from the Early Pleistocene of Venta Micena-2 (Spain) as "*Cervus*” *elaphoides*. However, according to Lister (1990), the small cervid from Venta Micena is a genuine and yet undescribed species. The fossil material from Venta Micena is quite poor and includes only fragmentary remains of antlers, upper and lower dentition, and limb bones. The antlers figured by Menendez (1987) are characterized by the high position of the first ramification (height of ramification is 2-3 times larger than the diameter of the antler base), the somewhat compressed lateromedially proximal part of the basal tine, and the accessory prong, which in one case is situated on the basal tine, and in another case is located in the area of the basal ramification. The antler beam is curved towards the posterior immediately above the basal ramification, and the pedicles are moderately long.

The enlisted antler characters approach the cervid under discussion to *R*. (*A*.) *ardei*, however, the deer from Venta Micena is somewhat smaller. According to Menendez (1987), the length of the upper tooth row of the deer from Venta Micena ranges from 81.3 to 84.1 mm (n=4), while the length of upper cheek teeth in *R.* (*A.*) *ardei*, according to Heintz (1970), varies between 97.5 and 109.0 (n=4). The dental morphology of the deer from Venta Micena is more advanced compared to *R.* (*A.*) *ardei*: P_4 is variable and in some cases is molarized; the upper premolar row is relatively short (the upper premolar to molar series ratio amounts to 65.8% in the sample from Venta Micena and to 78.8% and 73.9% in the samples of *R.* (*A.*) *ardei* described by Heintz 1970); the lingual cingulum in upper molars is reduced, however, the entostyle is large, flattened, and strong.

The cervid from Venta Micena and *R.* (*A.*) *ardei* are characterized by similar morphology of upper premolars: the hypocone and the protocone of P^2 and P^3 are separated, and the anterior wing of the hypocone of the upper premolars is supplemented with an additional enamel fold (Heintz, 1970: pl. XXXIV; Menéndez, 1987: 175, pl. 2, fig. 3). Therefore, the small cervid from Venta Micena is closely related to *R.* (*A.*) *ardei* but is distinguished by its smaller size and more advanced morphology of dentition. Most probably, the smaller deer from Venta Micena is a transitional form between *R.* (*A.*) *ardei* and the endemic deer *Haploidoceros mediterraneus* from the Iberian Middle and Late Pleistocene.

Subgenus *Rucervus* Hodgson, 1838

Diagnosis. The first tine is situated comparatively low above the burr; the height of the first ramification is less than twice the basal diameter of the antler; the crown part of the antler is relatively longer (no less than 40% of the antler beam length) and often is not palmated.

Type species: the subgenus is nominotypical.

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.

Rucervus (*Rucervus*) *gigans* Croitor, 2018.

Synonymy:

1997 *Megaloceros sp.*: Kostopoulos, p. 846, fig. 1-A, B, D, E, F.
2004 *Arvernoceros cf. verestchagini* David, 1992: Croitor and Kostopoulos, p. 140, figs. 1, 2, 4-A, 5.

Diagnosis. The body size is very large, being similar to that of the giant deer *Megaloceros giganteus*. The first ramification is situated quite close to the burr (the height of the ramification is less than 2 × DAP of the antler's base), flattened, and bifurcated, with the vertical orientation of the flattened portion and the fork. The angle of the first ramification is obtuse. The cross-section of the antler beam is circular. Pedicles are moderately long and somewhat deflected backwards, with a circular cross-section. The lower fourth premolar (P_4) is simple. The relative length of lower premolars is relatively long: the premolar/molar ratio normally exceeds 60%. Upper molars are supplemented with well-developed triangular entostyles, which are supplemented with a weak lingual cingulum at least in the M^3. Protoconal fold in the upper molars is not present. Mandibular diastema is somewhat shorter than the lower molar series. Metapodials are relatively long; the length of the metacarpus is comparable with that of the metatarsus

Differential diagnosis. The newly discovered species is notably larger than *R. simplicidens* and *R. colberti* found in the Siwalik fauna. *R. gigans* can be distinguished from *R. radulescui* by its significantly larger body size and the bifurcated first tine positioned lower on the anteromedial side of the antler's beam. Additionally, it can be differentiated from *Praemegaceros pliotarandoides*, also found in the same fauna, by its primitive unmolarized P_4, flattened and bifurcated first tine positioned close to the burr on the anterior side of the beam (as opposed to cylinder-shaped and inserted on the anteromedial side of the beam in *P. pliotarandoides*), the lack of vestigial subbasal tine, and a horizontal diastemal part of the mandible (as opposed to an elevated symphyseal part as seen in *Praemegaceros*). Furthermore, *R. gigans* is distinct from *R.* (*Arvernoceros*) *verestchagini* by its lower-positioned bifurcated first tine, which lacks the small palmation and trifurcation observed in the latter species.

Locus typicus. Apollonia-1, 60 km NE to Thessaloniki, Greece.

Stratum typicum: the fluviolacustrine sediments of Platanochori Formation (Premygdonian group), the final stage of the Lower Pleistocene, MNQ 20, 1.3–1.0 Ma.

Syntypes: The left hemimandible APL-384 with P_3-M_3 and destroyed ascending part; the left maxilla APL-274 with full cheek tooth series P^2-M^3; the basal fragment of antler APL-357 with almost complete basal tine and partially destroyed burr; the right metacarpus APL-385; the left metacarpus APL-334; and the frontal fragment with preserved basal portions of antlers APL-212. The syntypes are stored in the School of Geology of the University of Thessaloniki (Greece).

Description. The left mandibular ramus APL-384 (Fig. A.23) is exceptionally large, with a cheek tooth row length (L P_2-M_3, 188.0 mm) exceeding that of the *Megaloceros giganteus* sample stored in the NHML (L P_2-M_3, 161.1–173.1 mm, n = 12). Despite its size, the mandibular body is relatively low and not pachyostotic. The diastemal part of the mandible is relatively short, with a length slightly shorter than the lower molar series. P4 is simple, with a moderately extended anteroposterior metaconid. The fusion of the paraconid and parastylid of P_3 and P_4 forms a specific isolated enamel islet.

The mandibular fragment APL-33 belongs to an older individual with a deeply worn dentition, where M_1 is almost completely worn out. Its tooth row length (162.0 mm) falls within the variation range of the Irish sample of *M. giganteus* stored in the NHML. The entoconid and entostylid of P_4 are fused and close the little posterior valley, as in the deeply worn fourth premolars of *R. radulescui* from Liventsovka, although the anterior valley remains open.

The maxilla APL-274 (Fig. A.24) has a full row of cheek teeth in the advanced stage of wear, but meaningful morphological characters are still visible. The total tooth row length (157.1 mm) exceeds the size range of variation of *M. giganteus* from Ireland (L P^2-M^3, 141.6–153.3 mm, n = 9; stored in the NHML, MNHN, PMM, NHMB). The lingual wall of P^2 is cleft, separating its protocone and hypocone. The inner wall of the protocone of P^2 is folded. The lingual wall of P^3 has a shallow vertical groove, and the protocone and hypocone of P^3 are connected through an isthmus. The inner wall of the hypocone of P^3 is undulated, including a small enamel islet. The hypocone of P^4 includes a large enamel fold supplementing its inner wall. Upper molars are characterized by a well-developed hypoconal spur and flattened entostyles. In M^3, the entostyle is larger than in other molars and connected with a very small but clear lingual cingulum. The molar crowns are comparatively broad, with measurements of their breadth close to the values of the crown length.

The basal fragment of the shed antler APL-357 (Fig. A.25) is distinguished by the very low position of the basal tine and the obtuse angle of the first ramification. In contrast to *M. giganteus*, which also has a flattened and bifurcated basal tine, the flattened portion of the basal tine in *R. gigans* is oriented in the vertical plane.

The frontlet APL-212 (Croitor and Kostopoulos, 2004: fig. 14A) belongs to a relatively young individual with long, circular pedicles that point sideways and backward and are situated in the plane of the frontal bones. The angle of pedicle divergence is right. The sagittal profile of the frontal bones is prominent between the pedicles and slightly concave before the pedicles, while the frontal bones become concave in the sides of the interfrontal suture in the supraorbital area. The interfrontal suture is slightly elevated in front of the pedicles. The frontal part of the skull is relatively broad for the braincase breadth measured behind the pedicles, distinguishing the specimen from Apollonia-1 from the "large *Arvernoceros*" from Liventsovka with relatively narrower frontals. The antlers are characterized by a higher position of the basal tine compared to the previous specimen, indicating some degree of individual or ontogenetic variation of this character. The antler becomes strongly compressed lateromedially in the area of the first ramification, while the main beam cross-section is circular.

The postcranial bones are exceptionally large and can be distinguished from any cervid sample considered in the present study. A curious morphological feature of *R. gigans* that reflects its specific ecological niche as a high-level browser is the disproportionate length of its metacarpals, metatarsals, and radius for a deer of such large size, with lengths respectively 10.7%, 11.8%, and 4.2% longer than the corresponding mean lengths of the giant deer from Ireland (Croitor and Kostopoulos, 2004). The proportions of limbs in *R. gigans* are also peculiar, with its metacarpals comparable in length to the radius and metatarsus.

Genus *Haploidoceros* Croitor, Bonifay and Brugal, 2008

Nomenclatural acts: Bonifay (1967) originally described a few fragments of robust antlers from the Middle Pleistocene deposits (Mindel-Riss Interglacial, ca. 0.30-0.35) of Lunel-Viel (Southern France) as *Euctenoceros mediterraneus*. However, additional fossil material has since been discovered, revealing an advanced evolutionary specialization of cranial, dental, and antler morphology. These discoveries have led to the creation of a new monotypic genus, *Haploidoceros*.

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

Composition: the genus is monotypic.

Haploidoceros mediterraneus (Bonifay, 1967)

Diagnosis. A medium-sized deer, with an intermediate body size between fallow deer and red deer. The fully grown antlers are relatively robust and very long, bifurcating into two points. The antler beam is sickle-shaped, curved backwards and sidewards, and then upright and forwards. The cross-section of the antler beam is circular, with a rough and sculptured surface featuring longitudinal ribs and furrows. The basal tine is cylindrical and very long. The pedicles are very short, directed laterally and backwards, and have a circular cross-section. The neurocranium is relatively long. P^3 and P^4 have a cleft on their lingual wall, while the cingulum of the upper molars is reduced and in most cases ansent. Upper molars are characterized by the presence of an entostyle and a hypoconal spur, and P_4 is molarized. The upper and lower premolar series are relatively short.

Lectotype: unshed left antler LV-I-9-1179 connected to a fragment of the frontal bone, with destroyed distal portions of basal tine and beam (Fig. A.26). The specimen belongs to an adult male.

Paralectotypes: unshed right antler LV-I-9-980 with pedicle; unshed left antler LV-I-9-1594 with pedicle. Both specimens belong to adult male individuals. The specimens are figured by Bonifay (1967) and stored in the National Museum of Prehistory les Eyzies de Tayac (France).

Locus typicus. Lunel-Viel (Herault, France).

Stratum typicum: the Middle Pleistocene, Mindel-Riss Interglaciation.

Other localities: L'Igue des Rameaux (South-West France), Cova Del Rinoceront (the Iberian Peninsula).

Description. Large, massive, but simple antlers represent the most remarkable feature of this species. The robust fully grown antlers have only two points: the long sickle-shaped beam and the strong basal tine. The shed antler LV-IV-15728 (MNP) is the most complete specimen, preserving the main beam. The antler beam is very long (907 mm) and has almost the same diameter as the basal tine. Right above the bifurcation, it bends backwards and sidewards, then the antler curves uprights, and its distal portion is pointed forward. The transverse cross-section of the antler beam is mainly circular; the distal portion of the antler is slightly compressed mediolaterally. The basal tine is inserted high above the burr and is oriented along the axis of the antler base and pedicle. The base of the tine is somewhat compressed in the lateromedial direction. The distal portion of the tine has a regular circular cross-section. The individual variation of the antlers concerns the angle of the basal ramification, which varies in the sample from Lunel-Viel from 60° to 80°.

A similar specimen was discovered in the Late Pleistocene karst filling of the Cova del Rinoceront near Barcelona (Spain). This is a damaged skull with a complete left antler (Fig. A.27).

The pedicles are very short and robust, sloped backwards and sideward. The extremely short and robust pedicles in *H. mediterraneus* represent another remarkable distinctive character of this cervid. The pedicle height measured from the posteromedial side is approximately 1/3 of the pedicle diameter. The transverse cross-section of the pedicles has a regular circular shape. The neurocranium LV-IV-14911 (MNP) from Lunel-Viel is elongated, and unflexed, with slightly convex parietal and temporal bones. The body of the basioccipital is broad and bell-shaped. The *foramina ovale* are small, with an irregular rounded shape. The *bullae tympani* are large, rounded, somewhat compressed laterally, and prominent, with a rib and a rostral bony thorn. The occipital is comparatively low, with well-developed and prominent crests and ridges for nuchal muscles. The frontal bones are very broad (the estimated breadth is 120 mm) for the braincase breadth. The relatively broad frontals of *H. mediterraneus* are correlated with the sideward orientation of pedicles. The modern species *Rucervus duvaucelii* shows the greatest affinity in the proportions of the neurocranium with the skull from Lunel-Viel (Croitor et al., 2008).

The premolar series is comparatively short. The lingual wall of P^2 is cleft, so the hypocone and the protocone of P^2 are separated. The anterior wing of the hypocone has an internal enamel fold. The hypocone and the protocone of P^3 are separated as well. The anterior wing of the hypocone is supplemented with a large enamel fold projecting inward and backwards. The lingual wall of P^3 may be cleft (5 cases out of 21). The upper molars are characterized by the presence of an entostyle and a hypoconal spur (eperon). Only rudimentary remains of a cingulum are observed in M^2 and M^3 of some specimens. P_4 is always molarized. The upper and lower premolar series are relatively short (Fig. A.28).

The evolution of *H. mediterraneus* took place in the Iberian glacial refugium during the early Middle Pleistocene. *Rucervus* (*Arvernoceros*) *sp*. from the Early Pleistocene of Venta Micena-2 is the direct forerunner of *H. mediterraneus* that developed toward the molarization of P_4, the relative shortening of upper and lower premolar series, and the simplification of antlers. Pedicles became shorter and more divergent. Among the characters that indicate the phylogenetic relationship between R. (*A.*) *ardei* and *H. mediterraneus* we can mention the high position of basal ramification, the bending of the beam toward the posterior immediately above the basal ramification, the compressed proximal part of the basal tine that reminds the flattened basal tined in *Arvernoceros*, the circular cross-section of the antler beam, and the cleft lingual walls in upper premolars. The weak flattening of the distal part of the beam observed in the specimen LV-IV-15728 may be interpreted as a vestige of distal palmation of *Arvernoceros*.

Abundant remains of *H. mediterraneus* were also reported from the Late Pleistocene of Cova Del Rinoceront, Iberian Peninsula (Sanz et al., 2014), thus confirming the importance of the Iberian glacial refugium for the evolution of this endemic cervid. The Iberian material shows essentially the same morphology as the sample from the type locality.

Genus *Sinomegaceros* Dietrich, 1933

Sinomegaceros insolitus (Vekua, Bendukidze and Kiladze, 2010)

Comments. A newly discovered large-sized deer species with palmated antlers was described from the Early Pleistocene of Dmanisi (Georgia). The holotype is a shed antler with very long terminal tines and a palmation supplemented by several smaller posterior crown tines (Fig. A.29 A). The basal tine is situated close to the burr (Vekua et al., 2010). The antler structure is similar to that of "*Dama*" *sericus* Teilhard de Chardin and Trassaert, 1937, a much smaller deer from the Pliocene of Shansi (China). The palmation of this Caucasian deer also shows an affinity to *Praemegaceros* (*Nesoleipoceros*) *solilhacus*. However, *S. insolitus* is distinguishable by its strong development of the basal tine and the absence of the middle tine (Fig. A.29). The fragment of antler palmation from Dmanisi reported by Krijgsman et al. (2019: fig. 11) as *Cervalces* cf. *gallicus* actually belongs to *S. insolitus*.

Sinomegaceros stavropolensis (Titov and Shvyreva, 2016)

Comments. Described from the Early Pleistocene (Late Villafranchian) of Ciscaucasia, this medium-sized deer (DLM above burr measuring 60.7 mm) is similar to the previous species, but can be differentiated by its higher basal tine, short terminal tines, and more robust palmation with posterior tines. The antler beam cross-section is subtriangular, which distinguishes it from *R*. (*Arvernoceros*) *ardei* and *R*. (*Arvernoceros*) *verestchagini*, characterized by a circular beam cross-section. According to Titov and Shvyreva (2016), this species is considered a transitional form between *R*. (*Arvernoceros*) *ardei* and *Megaloceros giganteus*. The antler shape of *Sinomegaceros starvopolensis* shows a striking similarity with "*Dama*" *sericus* and Asian *Sinomegaceros*, while the resemblance with *M. giganteus* is less evident. In contrast to *Megaloceros*, the basal antler is located at a distance from the burr, and the middle tine is absent. The fragment of antler palmation from the Early Pleistocene of Dmanisi (Georgia) reported by Krijgsman et al. (2019: fig. 11) as *Cervalces* cf. *gallicus* is similar to *Sinomegaceros starvopolensis*. These findings suggest that *S.* insolitus and *S. stavropolensis* may be closely related forms.

Genus *Eucladoceros* Falconer, 1868

Synonymy:

Euctenocerus Trouessart, 1899
Eucladocerus Simpson, 1945
Polycladus Crozet et Jobert 1828 /Gervais ?/

Nomenclatural acts: The name *Eucladoceros* was first introduced in the second volume of the posthumous notes of H. Falconer (edited by C. Murchison) as a subgenus for the fossil cervid species from the "Forest-bed" of the Norfolk coast at Backton (England) called *Cervus* (*Eucladoceros*) *sedgwickii* (Gun.) (Falconer, 1868: p. 472). While Falconer (1868) attributed the authorship of the species to Mr Gunn, who was the owner of the fossil specimen, the species authorship belongs to Falconer since Gunn's antler description written in 1863 was never published (Falconer, 1868: p. 471, editor's footnote).

Falconer (1868) also used the species name *Cervus* (*Rusa*) *eucladoceros* (Nob.) for a large modern deer from India with upper canines and a basal tine forming an obtuse angle with the antler beam and "quardifurcate" distal portion of the antler. As correctly noted in the editor's footnote, *Cervus* (*Rusa*) *eucladoceros* is a synonym of the modern *Rucervus duvaucelii* (Cuvier, 1825) (Falconer, 1868: p. 587).

Trouessart (1898) included several species in the genus *Eucladoceros*, such as *Cervus polycladus* Gervais, 1852 (a synonym of *Croizetoceros ramosus* Croizet and Jobert, 1828), *C.*

ardeus Croizet and Jobert, 1828 (later included in the genus *Arvernoceros* Heintz, 1970), *C. sedgwickii* Falconer, 1868 (= *C. intermedius* de Serres *fide* Trousseart, 1898), *C. ctenoides*, *C.* dicranius (*sic*!), *C. macroglochis* Pomel, 1851 (considered a *nomen nudum* by Heintz, 1970: p. 182). In the same publication, Trouessart (1898: 880) proposed a new subgenus, *Euctenoceros*, within *Cervus* with a single species *C. tetraceros* Dawkins, 1878, giving, therefore, formal taxonomical status to Lydekker's (1885) "tetracerotine group".

Teilhard de Chardin and Piveteau (1930: p. 53) recognized a specific for *Eucladoceros* comb-like antler plan construction and proposed a diagnosis for *C.* (*Eucladoceros*) based mostly on antler morphology of *Eucladoceros boulei* (Nihowan, Northern China): “bois munis de nombreux andouillers (de quatre à six), longs, souvent aplatis et bifurqués, parfois soudés, disposés en avant de la perche et normalement à elle, comme les dents d’un peigne. Premier andouiller naissant près ou loin de la meule. Quatrième premolaire simple ou molarisée“.

Simpson (1945: p. 154) raised Falconer's *Eucladoceros* to the rank of genus and included *Polycladus* Pomel, 1854 in the synonymy of this genus. Azzaroli (1947, 1953) objected to the use of the name *Eucladoceros* Falconer due to potential confusion with a homonym. He proposed to replace *Eucladoceros* Falconer with the genus name *Euctenoceros* Trouessart, 1898 (based on the genus type *Cervus tetraceros* Dawkins, 1875) to avoid taxonomic confusion. However, there is no homonymy between Falconer's subgenus *Eucladoceros* and the species *Cervus* (*Rusa*) *eucladoceros*, as they represent the genus-group and species-group names, respectively.

Diagnosis: Body size is similar to modern red deer. The first antler tine is situated at a certain distance from the burr. A small additional prong is present on the medial side of the beam, near or above the first ramification. The beam segment between the first and second tine is cylindrical in shape. The distal part of the beam above the second tine and all crown tines, including the second tine of the antler, are more or less compressed from the sides. The crown portion of the antler consists of 3-5 crown tines and has a comb-like shape, with all tines inserted on the upper side of the beam. The basioccipital is broadened in the area of pharyngeal tuberosities, bell-shaped. The orbitofrontal part of the skull is short, with the anterior edge of the orbit situated above the third molar (M^3). The praeorbital fossae are relatively large and deep. The nasal bones are short and do not extend beyond the line connecting the anterior edges of orbitae. Small upper canines are present. The upper molars may have additional enamel folds on the protocone and hypocone. The lingual wall of P^2 is cleft or grooved. Hypocons of P_3 and P^4 are supplemented with additional inner enamel folds. P_4 is variable, but more often is not molarised.

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.

Eucladoceros dicranios (Nesti, 1841).

Synonymy:

1841 *Cervus dicranios* Nesti: Savi and Sismonda, p. 159.
1849 *Cervus martialis* sp. nov.: Gervais, p. 189.
1859 *Cervus* (*Tarandus*) *martialis* Gervais, 1849: Gervais, p.144, Pl. 21, Figs. 2-5.
1868 *Cervus* (*Eucladoceros*) *sedgwickii* sp. nov.: Falconer, p. 472.
1881 *Cervus dicranius* Nesti, 1841: Rütimeyer, p. 106, Tab. 1, Fig. 1.
1891 *Cervus segdwickii* Falconer, 1868: Newton, p. 31.
1898 *Anoglochis segdwicki* Falconer: Lydekker, p. 240, fig. 66.
1898 *Cervus* (*Eucladoceros*) *sedgwickii* Falconer, 1868: Trouessart, p. 883.
1898 *Cervus* (*Eucladoceros*) *dicranius* Nesti, 1841: Trouessart, p. 884.
1962 *Cervus* (*Eucladocerus*) *sedgwiki* Falconer, 1868: Godina et al., p. 373.
1893 *Cervus* (*Polycladus*) *segdwicki* Falconer, 1868: Zittel, p. 402, figs. 334, 335.
1953 *Euclenoceros dicranios* (Nesti, 1841) : Azzaroli, p. 38.

Nomenclatural acts: The species name Cervus dicranios was first mentioned in a publication by Savi and Sismonda (1841) summarizing Filippo Nesti's oral communication about several new fossil deer species from Valdarno Superiore and Val di Chiana during a scientific meeting held in Florence (Azzaroli and Mazza, 1992a).

Diagnosis: The basal tine is flattened and branched. The crown tines are bifurcated or trifurcated.

Holotype: antlered skull IGF270, MGUF (Azzaroli and Mazza 1992a: pls. 1, 2).

Locus typicus: Upper Valdarno, Tuscany, Italy.

Stratum typicum: Late Villafranchian deposits of Upper Valdarno.

Description. This is the most advanced and possibly the largest (300 kg) species of the genus, characterized by the particularly complicated morphology of antlers (Fig. A.31 E). The first tine is situated at a certain distance from the burr, with an accessory specific to the genus, a subulate tine, located in the area of the first ramification somewhat medially (it is directed upright on the antlered skull). The three crown tines are inserted on the anterior side of the antler beam. The skull is characterized by well-developed preorbital pits, large ethmoidal openings with long contact with the nasal bone, and a flexed braincase when compared to other forms of *Eucladoceros*. The advanced braincase flexion permits us to ascribe the damaged skull IGF255 (MGUF) from Upper Valdarno to *E. dicranios* (Fig. A.30).

The antler beam and tines (with the exception of the accessory subulate tine) are strongly compressed from the sides. The antler tines are bifurcated or trifurcated, resulting in the right antler having 14 points and the left one having 12 points (de Vos et al., 1995). In *E. dicranios*, the bifurcation of antler tines represents a sort of hypermorphosis, which is particularly evident in the proximal tines: the first (brow) tine and the first crown tine are flattened and trifurcated. The trifurcation of the first crown tine on each antler resulted from the subsequent bifurcation of the anterior branch of the tine. The second crown tine splits into a bifurcation in its proximal part and forms two very long ramifications. The anterior ramification on the right antler is supplemented with an accessory short prong. The third crown tine forms a smaller bifurcation in its distal portion. The distal tine of the right antler is also bifurcated. The crown tines are somewhat deflected backwards. The antler beams are curved sideways, giving the antlers a peculiar "brushy" appearance. This optical illusion caused the incorrect description of the antler shape as "brush-like," as reported, for instance, by Geist (1998), while the taxonomically significant comb pattern of antler construction was overlooked.

Eucladoceros dicranios is quite rare in the paleontological record of Europe, with its known distribution ranging from the Azov Sea area in the east to England in the west (de Vos et al., 1995). The findings from Italy, England, and Russia display some minor morphological differences (Azzaroli and Mazza, 1992a; de Vos et al., 1995); however, it is impossible to estimate the significance of these differences since only one complete specimen is available from each locality. Baygusheva and Titov (2013) described the sample from the Lower Pleistocene (Middle Villafranchian) of Liventsovka (Azov Area, Russia) as the new subspecies *E. dicranios tanaitensis*, which is considered a direct forerunner of *Praemegaceros pliotarandoides*, regarded by some authors as *E. orientalis pliotarandoides* (De Alessandri, 1903) and *E. orientalis orientalis* (Radulesco and Samson, 1967). The type specimen of *E. dicranios tanaitensis* is an incomplete right antler (Baygusheva and Titov, 2013: fig. 2b-c) with the rather well-preserved first known tine, which is dichotomously branched into four prongs, and the proximal part of the second crown tine. The distal part of the antler is destroyed. This incomplete preservation of the antler from Liventsovka gives a wrong impression of affinity with the dichotomously branched crown tines of *P. pliotarandoides* antlers, which, however, lack such important diagnostic character of *Eucladoceros* as the comb-like bauplan.

It is also important to note that *Cervus pliotarandoides* De Alessandri, 1903 has priority over *Psekupsoceros orientalis* Radulesco and Samson, 1967.

.

Eucladoceros ctenoides (Nesti, 1841)

Synonymy:

1841 *Cervus ctenoides* Nesti: Savi and Sismonda, p. 159.
1841 *Cervus orticeros* Nesti: Savi and Sismonda, p. 159.
1898 *Cervus* (*Eucladoceros*) *ctenoides* Nesti, 1841: Trouessart, p. 884.

Nomenclatural acts: The species names *Cervus ctenoides* and *Cervus orticeros* were first mentioned in a summary of Filippo Nesti's oral communication on fossil deer species presented at a scientific meeting in Florence, published by Savi and Sismonda in 1841. Azzaroli (1953) and Azzaroli and Mazza (1992a) have included *Cervus orticeros* as a synonym of *Cervus ctenoides*. This polymorphic species is represented by several local and chronological forms mainly distinguished by morphological details of antlers (Azzaroli and Mazza, 1992a; De Vos et al., 1995). Many authors nowadays place numerous species names such as *senezensis*, *darestei*, *falconeri*, *tegulensis*, and *tetraceros* in the list of synonyms of *Eucladoceros ctenoides* (De Vos et al., 1995; Croitor and Bonifay, 2001; Valli and Palombo, 2005; Baygusheva and Titov, 2013).

Diagnosis: The first tine is unbranched and has a circular cross-section. The crown tines are typically simple and unbranched, with only occasional bifurcation seen in the distalmost crown tines.

Holotype: right antler IGF 377, MGUF.

Locus typicus: Upper Valdarno, Tuscany, Italy.

Stratum typicum: Late Villafranchian deposits of Upper Valdarno.

Description. The body size of this species (250 kg) is slightly smaller than that of *E. dicranios* from Upper Valdarno, making it difficult to distinguish mandibles and postcranial remains of these two species. The first tine of *E. ctenoides* antlers is cylindrical and unbranched, located at a certain distance from the burr. A small accessory tine is located on the anteromedial side of the beam in the area of the first ramification, often preserved as a knob-like vestige. The antler beam is slightly compressed from the sides between the first and second tine and becomes strongly compressed above the second tine. The crown tines form a right angle with the beam and are situated on its anterior side. Some specimens from the type locality are characterized by ossacional dichotomous branching of crown tines. Similar spontaneous dichotomy of crown tines is observed in antlered skulls of *Eucladoceros* from Sénèze (France) stored in Paris and some antlers from Olivola (Italy) (Azaroli, 1948). The species includes several subspecies distinguished mostly by the shape of their crown.

Distribution. Early Pleistocene of Western Europe and the Balkan Peninsula.

Subspecies:

Eucladoceros ctenoides ctenoides (Nesti, 1841)

Description: nominotypical subspecies. The crown tines are straight with slight undulations. The antler shape overall displays a distinct comb-like pattern. Azzaroli and Mazza (1992a) noted that the fourth tine of the holotype of *E. ctenoides* exhibits a dichotomous bifurcation that is clearly discernible. Additionally, the fifth tine also shows dichotomous branching (Fig. A.31 A).

Distribution: Early Pleistocene of Western Europe, Late Villafranchian of Upper Valdarno (Italy). A similar form of *Eucladoceros* is reported from the final stage of Late Villafranchian from Ceyssaguet, France (Croitor and Bonifay, 2001).

Eucladoceros ctenoides olivolanus Azaroli and Mazza, 1992

Synonymy:

1947 *Cervus* (*Euctenoceros*) *ctenoides* (Nesti, 1841): Azzaroli, fig. 8.
1953 *Euctenoceros dicranios* (Nesti, 1841): Azzaroli, p. 38.
1992 *Eucladoceros dicranios olivolanus* ssp. nov.: Azaroli and Mazza, p. 50, fig. 7.

Nomenclatural acts: Azaroli and Mazza (1992a) proposed a new subspecies for the sample from Olivola, which they believed to be a mixture of characteristics from *E. ctenoides* and *E. dicranios* and considered it to be an ancestor of those two species.

Diagnosis: distal crown tines show a more frequent bifurcation than the nominotypical subspecies.

Holotype: distal portion of antler IGF1402 (MGUF) with three crown tines.

Locus typicus: Olivola, Tuscany, Italy.

Stratum typicum: Late Villafranchian.

Description. The distal parts of two out of three crown tines in the type specimen are bifurcated, resembling to some extent *E. dicranios*. However, the basal tine in *Eucladoceros* from Olivola (seen in other specimens) is cylinder-shaped and unbranched like in *E. ctenoides* (Fig. A.31 C). Although occasional incipient bifurcation in crown tines is characteristic of *E. ctenoides*, this unstable crown tine bifurcation should be regarded as a hypertrophy rather than a transitional evolutionary stage between *E. ctenoides* and *E. dicranios*. Therefore, *E. dicranios olivolanus* is a junior synonym of *E. ctenoides*, or at least should be kept as the subspecies *E. ctenoides olivolanus*. Unlike the antler hypermorphology in *E. dicranios*, thich is characterized by the largest and most branched first crown tine, the antler hypertrophy in *E. ctenoides ctenoides* is more strongly expressed in the distal crown tines (second and third) that tend to be bifurcated.

Distribution. Early Pleistocene (ca. 2.0 Ma) of Central Italy.

Eucladoceros ctenoides falconeri (Dawkins, 1868)

Synonymy

1868 *Cervus falconeri* sp. nov.: Dawkins, p. 517, pl. XVIII, figs. 9-12.
1891 *Cervus falconeri* Dawkins, 1868: Newton, p. 28, Pl. IV, fig. 7a-b.
1898 *Cervus* (*Dama*) *falconeri* (Dawkins, 1868): Trouessart, p. 885.
1904 *Cervus teguliensis* sp. nov.: Dubois, p. 218, fig. 1
1904 *Cervus tegulensis* sp. nov.: Dubois, p. 247, fig. 1.
1910 *Cervus senezensis* sp. nov.: Deperet and Mayet, p. 261.
1931 *Cervus darestei* sp. nov.: Deperet, p. 1256.
1946 *Eucladoceros tegulensis* (Dubois, 1904): Schreuder, p. 155.
1953 *Euctenoceros falconeri* (Dawkins, 1868): Azzaroli, p. 38.
1970 *Eucladoceros senezensis senezensis* (Deperet and Mayet, 1910), Heintz, p. 186, pls. X-XIII, fig. 202.
1992 *Eucladoceros tegulensis* (Dubois, 1904): Spaan, p. 24, fig. 1.
1995 *Eucladoceros ctenoides* (Nesti, 1841): de Vos et al., p. 104, fig. 8, p. 109.
1970 *Eucladoceros teguliensis* (Dubois, 1904): Heintz, p. 186, fig. 199.
1995 *Eucladoceros ctenoides* (Nesti, 1841) : de Vos et al., p. 109.

Nomenclatural acts: Lydekker (1885: 91) placed *Cervus falconeri* Boyd-Dawkins in the so-called "Damine group" (fallow deer group) and suggested a relationship with *Cervus browni* (= *Dama clactoniana* Falconer), noting that the antlers of the former cervid were "much less palmed". This view was shared by Newton (1891) and Trouessart (1898), who included *Cervus falconeri* in the genus *Dama*. De Vos et al. (1995) regarded *Eucladoceros falconeri* (Dawkins, 1868), *E. senezensis* (Deperet and Mayet, 1910), and *E. tegulensis* (Dubois, 1904) as synonyms of *E. ctenoides* (Nesti, 1841). Lister (1998) observed that the antler sample of *Eucladoceros* from Norwich Crag represents a distinct morphotype, and therefore suggested that the species name *E. falconeri* be maintained.

Diagnosis: The accessory prong is well-developed and situated at a certain distance from the first ramification. The beam segment between the basal tine and crown part is relatively longer than in nominotypical subspecies. Crown tines are bent inward and forward.

Holotype: right shed antler of a young individual BM33509. The distal part of the antler above the first crown tine is not preserved.

Locus typicus: Norwich Crag, England.

Stratum typicum: "Pliocene of Norwich Crag" (Dawkins, 1868).

Description. The type antler most probably belongs to a young individual (De Vos et al., 1995). The antler base is irregularly rounded, with a DAP of 33.7 mm and a DLM of 29.2 mm. The antler circumference at the base is 108 mm. The first tine of the type specimen is situated 76.7 mm from the burr. The accessory prong is located on the anteromedial side of the antler beam. The length of the beam segment between the basal tine and the first crown tine is 20 cm. The antler beam is compressed from the side in this part of the antler and becomes more flattened above the first crown tine. The shed left antler M15696 from Norwich Crag, Dunwich, Suffolk, is larger (DAP above the burr, 42.7 mm; DLM above the burr, 40.0 mm; CFR, 125 mm). The first ramification is situated at 75.0 mm from the burr, and the accessory prong is very strong, pointed medially, and situated at 81.0 mm from the first tine.

The complete antlers from Sénèze, the type locality of *Cervus senezensis*, are characterized by a somewhat less pronounced metamerism, which represents an advanced specialization (Fig. A.31 B). The skull of *E. ctenoides* from Sénèze is characterized by a braincase that is slightly flexed, well-developed preorbital pits, and large ethmoidal openings that are bordered by nasal bones with a short interval, comprising only around 30% of the length of the ethmoidal opening. Additionally, the oval bullae tympani feature a longitudinal ridge, and the basioccipital widens in pharyngeal tuberosities, giving it a broad, bell-shaped appearance (Fig. A.32). The posterior edge of the nasal bones almost reaches the line connecting the anterior edges of the orbits.

The dentition is generally primitive: the P_4 is normally not molarized, the lower premolar series is moderately short (premolar/molar ratio varies between 55% and 67%), the upper molars occasionally are supplemented with a small protoconal fold and a hypoconal spur, and the entostylids are small. Although upper canines are likely present, they could not be confirmed as all specimens I studied were damaged in their rostral part.

Distribution. Early Pleistocene of England, France, the Netherlands, Germany, and Romania.

Eucladoceros ctenoides tetraceros Dawkins, 1878

Synonymy:

1853 *Cervus macroglochis* Nob.: Pomel, p. 104 (nomen nudum).
1878 *Cervus tetraceros* Dawkins: Dawkins, p. 416, figs. 13, 14, 15, 16, 17.
1891 *Cervus tetraceros* Mackie 1861: Newton, p. 32, Pl. IV, fig. 2.
1898 *Anoglochis tetraceros* (Dawkins, 1878): Lydekker, p. 242, fig. 67.
1952 *Euctenoceros tetraceros* (Dawkins, 1878): Bout and Azzaroli, p. 14, figs. 3, 4, 5, 6, 7.

Nomenclatural acts: In 1853, Pomel provided the first description of the comb-like antlers of the large-sized deer from Peyrolles (Puy-de-Dome, France). He proposed the species name *Cervus macroglochis* and provided a brief description of the antlers. Unfortunately, Pomel did not include any figures, and the fossil collection used for the species description was lost (Bout and Azzaroli, 1952). Consequently, the species *Cervus macroglochis* is now considered a *nomen nudum* (Heintz, 1970).

Bravard's collection of fossils from Peyrolles had better fate. According to Newton (1891), NHML purchased a series of cervid remains from Peyrolles in 1852, several of which were large shed antlers labelled by Bravard as "*Cervus tetracoceros*". However, Bravard did not publish a formal description of the species. The cervid fossils from Peyrolles were eventually described by

Mackie (1861), who used Bravard's proposed species name. Newton (1891) attributed the species authorship to Mackie. This species name should be considered *nomen oblitum*.

Dawkins (1878) later proposed a modified name for the species, *Cervus teraceros*, and published a detailed description with measurements and figures of the antlers. He suggested that *C. tetraceros* was closely related to *Cariacus virginianus* (= *Odocoileus virginianus*), a viewpoint also shared by Lydekker (1885: p. 113; 1898: p. 242). However, this conclusion was based on a superficial similarity of the comb-like pattern of the distal antler portion. It is worth noting that in Eucladoceros, the crown tines are inserted on the anterior side of the beam, while in *Odocoideus*, the crown tines are situated on the posterior side of the beam. Lydekker (1898: fig. 67) believed that the antlers from Peyrolles were deformed and proposed a reconstruction resembling the antlers of *Odocoileus*. However, this reconstruction is incorrect. Azzaroli (1952) selected the lectotype from Bravard's collection stored in NHML.

Diagnosis: The basal tine is very long, as long as the first crown tine. The crown tines never bifurcate and are bent in their distal parts toward the posterior.

Lectotype: shed complete left antler M34409 (NHML).

Locus typicus: Peyrolles, France.

Stratum typicum: Late Villafranchian of Peyrolles.

Description. The antlers of this species are generally thin, with a remarkably elongated distal portion (Fig. 3.31 E). The shape of the lectotype antler base is circular. The basal tine is cylindrical and very long, while the beam segment between the basal and the first crown tine is also cylindrical, and the distal part of the beam is flattened. The distance between the basal and first crown tines is longer than the distance between the crown tines themselves. The crown tines are flattened and their distal portions are bent backwards, but they do not show any tendency towards dichotomic bifurcation. The accessory prong in the area of the first ramification is not developed. The total length of the antler reaches 75 cm, with the apical part being very long and comprising one-third of the total antler length.

Distribution. Early Pleistocene of France.

Eucladoceros aff. *boulei* Teilhard de Chardin and Piveteau, 1930

Comments. This cervid species is represented by an almost complete antler with a damaged basal part and some other fragments of antlers that originate from the Early Pleistocene of Kapetanios, Greece (Steensma, 1988). The crown part of the antler shows a striking resemblance to Eucladoceros boulei from Nihowan, China, with flattened, lobe-like crown tines that have varying distances between them (Fig. A.33 F). It is unclear whether Eucladoceros from Kapetanios is directly related to European forms, or represents a dispersal event from China, and therefore has a sister relationship with *E. dicranios* and *E. ctenoides*. Perhaps *Eucladoceros* from Kapetanios should be considered at least a new subspecies of *Eucladoceros boulei*.

Genus *Praemegaceros* Portis, 1920

Synonymy:

Praerangifer Portis, 1920
Orthogonoceros Kahlke, 1956
Tamanalces Verestchagin, 1957
Allocaenelaphus Radulesco and Samson, 1967
Psekupsoceros Radulesco and Samson, 1967
Nesoleipoceros Radulesco and Samson, 1967

Nomenclatural acts. Portis (1920) proposed *Praemegaceros* as a subgenus of the genus *Cervus*, with a single species, *C.* (*Praemegaceros*) *dawkinsi* Newton, 1882. Decades later, Kahlke (1956) introduced the genus *Orthogonoceros* with the type species *Cervus verticornis* Dawkins. Kahlke (1965) later recognized the priority of Portis' (1920) *Praemegaceros*. The genus was first reviewed by Radulescu and Samson (1967), who proposed the genus definition and designated *Cervus dawkinsi* Newton as the type species. In the same publication, Radulescu and Samson (1967) proposed the new genera *Allocaenelaphus*, *Psekupsoceros*, and *Nesoleipoceros*, which are synonyms of *Praemegaceros* sensu Kahlke (1965) (Croitor, 2006a). The genus includes several Early and Middle Pleistocene continental giant forms, with an estimated body mass ranging between 300 and 500 kg, and two lineages of medium-sized or even dwarfed forms that survived in insular and/or refugial isolation on the Corso-Sardinian Massif and the island of Great Britain. Radulescu and Samson (1967) and Azzaroli and Mazza (1993) regarded the genus *Eucladoceros* as a forerunner of *Praemegaceros*, seeking support for this hypothesis in the analogous general construction of antlers. *Praemegaceros* is distinguished from *Eucladoceros* by its larger body size and complicated shape of antlers that never show the metameric bauplan. The advanced Middle and Late Pleistocene species of *Praemegaceros* are characterized by significant anteroposterior compression of pedicles and their stronger divergence. The basal tines are reduced, sometimes represented by vestigial rudiments or completely vanished, while their distal parts are expanded into variously shaped palmations (Azzaroli, 1979; Croitor, 2006a). The mosaic combination of morphological details of antlers and teeth suggests that *Praemegaceros* is a paraphyletic group that includes three more or less closely related lineages.

Diagnosis: Deer of medium to very large size. The skull is characterized by flat or transversally convex frontal bones before pedicels, which are bordered by a bonny ridge, ranging from the coronal suture to the supra-orbital openings. The antlers are robust and very divergent in their proximal portion; the distal part of antlers is oriented parasagittally as a rule. The subbasal tine, if not reduced, is always unbranched with a circular cross-section. The posterior tine of the antler is developed. The braincase is short and broad behind pedicles; the basioccipital is broad and bell-shaped; the nasal bones do not extend behind the line connecting the anterior edges of orbits; the upper and lower premolar series are relatively long; the cingulum in upper molars is not developed; the mandibular pachyostosis is not developed and lower jaw maintains the normal proportions. The molarisation of lower P_4 may be variable. The antlers are strongly divergent; the antler crown is not metameric.

Distribution: Pleistocene; Europe, Near East, Transcaucasia, Central Asia.

Subgenus *Praemegaceros* Portis, 1920

Diagnosis. The antler beam is set obliquely to the antler burr. The subbasal tine resting on the antler burr is present as a rule; it may be well-developed or vestigial. The laterally inserted basal tine is never developed. The dorsal tine is in the medial position to the subbasal tine (the dorsal position if the antler beam is in the natural orientation on the skull). It may be very large or vestigial. A well-expressed rib extends from the subbasal tine to the dorsal one. The antler beam is straight in the area of the dorsal tine. The subbasal tine and the middle tine are oriented in the same plane on the anterior side of the antler beam. The upright curvature of the antler beam in the area of the posterior tine is present only in the archaic species. The lower fourth premolar is molarised as a rule. Molars are devoid of the lingual cingulum and the protoconal fold.

Type species: *Cervus dawkinsi* Dawkinsi, 1882.

Praemegaceros (*Praemegaceros*) *obscurus* (Azzaroli, 1953)

Synonymy:

1953 *Cervus obscurus* sp. nov.: Azzaroli, p. 74-75, fig. 42-45.
1967 *Allocaenelaphus arambourgi* sp. nov. et gen. nov.: Radulesco and Samson, p. 324, fig. 1.
1977 *Eucladoceros cf. tetraceros* (Dawkins): Aleksejeva, tab. 20.
1979 *Megaceros* (*Megaceroides*) *verticornis* (Dawkins): Azzaroli, p. 7.
1992 *Megaceroides boldrinii* sp. nov.: Azzaroli and Mazza, p. 29, fig. 4.
1995 *Megaceroides obscurus* (Azzaroli): Abbazzi, p. 224.
1995 *Megaceroides arambourgi* (Radulesco and Samson): Abbazzi, p. 229.
2001 *Praemegaceros obscurus* (Azzaroli): Croitor and Bonifay, p. 132.

Nomenclatural acts. Azzaroli (1953) described "*Cervus*" *obscurus* as a species with an uncertain taxonomic position, based on a series of syntypes: a fragment of antler (M2321) (NHML) (Azzaroli 1953: 74, fig. 42), an antler tine (M6421) (NHML) (ibidem, fig. 43), and a basal fragment of antler with pedicle and frontal bone (M18482) (NHML) (ibidem, p. 75, fig. 44a-b). However, the original species description did not provide an explicit diagnosis.

This deer has been known by several species names. Radulescu and Samson (1967) described a new genus and species, *Allocaenelaphus arambourgi*, from the early Pleistocene of Rotbav-Silvestru (Romania). The holotype of *A. arambourgi*, RS-1 (IS), is a left antler with the frontal part of the skull. The antler is large and heavy, with a strong subbasal tine resting on the burr, a straight beam compressed from the sides, a medially inserted dorsal tine that curves toward the anterior, and a middle tine situated on the anterior side of the beam. The pedicles are strong, robust, and cylindrical, with a bony ridge bordering the pedicle base from the medial side. Radulescu and Samson (1967) created this new genus and species to emphasize its transitional position between *Eucladoceros* and *Praemegaceros*. They believed that the deer from Rotbav-Silvestru had eucladocerine characters such as a straight, compressed beam from the lateral sides, a strong subbasal tine, and the position of the second and third tines, as well as praemegacerine characters like the large angle of divergence between antlers (≤ 90º) and the dorsal tine that curves toward the anterior. Interestingly, the morphology of *A. arambourgi* described by Radulescu and Samson (1967) matches that of *P. obscurus* precisely. Therefore, *A. arambourgi* is a junior synonym of *P. obscurus*.

A unique partial skeleton of a young male, with an almost complete but badly deformed antlered skull, was discovered in the latest Villafranchian of Pietrafitta. Azzaroli and Mazza (1992) described the specimen as a new species, *Megaceroides boldrinii*, which they believed represents a transitional form between *Eucladoceros* and *P. verticornis*. Azzaroli and Mazza (1995) echoed the ideas of Radulescu and Samson (1967) in arguing for the establishment of both *A. arambourgi* and *M. obscurus*, as the definition of these species is similar. Abbazzi (1995) restored the validity of "*Cervus*" *obscurus* Azzaroli, 1953 as a species name and designated specimen M2321 as a lectotype (Abbazi 1995: p. 224, fig. 2), leading to the inclusion of *Megaceroides boldrinii* in the synonymy of "*C.*" *obscurus*. However, the lectotype choice raises another taxonomic issue, as the type locality must be indicated according to the lectotype. Unfortunately, the collection label of lectotype M2321 only gives vague information about the locality, indicating "Forest Bed, Norfolk". The labels of the syntypes M6421 and M18482 (paralectotypes) indicate the sites Overstrand and Mundesley, respectively.

Diagnosis: The body size is very large. The antler base is set obliquely to the burr plane. The subbasal tine is long, strong, cylindrical, and situated very close to the burr. The dorsal tine is situated on the upper (medial) side of the beam, very long and compressed in the dorsoventral direction in its distal part. The middle tine appears in fully mature individuals and is set on the anterior side of the beam. The posterior tine is developed in adult individuals. The antler beam is sharply bent in the area of the posterior tine. The distal portion of the antler is not palmed. Pedicles are cylindrical, with normal orientation. The preorbital fossae are large and deep. The ethmoidal openings are large. The anterior part of the maxillary bones is moderately extended. The lingual wall of P^2 is cleft. The lower fourth premolar (P_4) is molarised.

Lectotype. The NHML specimen M2321 belongs to a mature male and consists of a proximal fragment of the left antler attached to a pedicle with a considerable portion of the frontal bone. The antler beam is oriented obliquely to the burr and the preserved portion of the beam is straight, compressed from the lateral sides, with a slightly undulated ventral surface. The subbasal tine is located very close to the burr and directed towards the anterior, forming a very obtuse angle (approximately 110º) with the antler beam. The dorsal tine springs off on the dorsal surface of the beam at a certain distance from the subbasal tine. It has a circular basal cross-section and is curved towards the anterior. There is a small accessory tip on the dorsal side of the beam between the basal and the second tines. The pedicle is short and massive, with a circular transverse section, and the frontal bone is somewhat depressed between the pedicle and the frontal suture. A bony rib borders the medial side of the pedicle base. The antler surface has longitudinal shallow furrows and ribs. The circumference of the pedicle is 190 mm, the anteroposterior diameter of the pedicle is 58.1 mm, the anteroposterior diameter of the burr is 88.2 mm, and the height of dorsal tine insertion is 147.8 mm.

Locus typicus: Forest Bed, Norfolk, England.

Stratum typicum: Forest Bed Formation, Early or Middle Pleistocene.

Paralectotypes. The specimen M6421 is a dorsal tine that is gently bent with a distal portion that is compressed dorso-ventrally and ends in a flat rounded termination. The tine has a length of 340 mm and a circumference at the base of 130 mm. The dorsoventral diameter of the tine base is 35.4 mm, while its mediolateral diameter is 41.7 mm. The breadth of the tine termination is 36.7 mm. The specimen M18482 is slightly larger than the lectotype, with a pedicle circumference of 210 mm and a maximal diameter of 68.2 mm. The height of dorsal tine insertion measures 117.5 mm.

Description. The antlers of *P. obscurus* are easily recognizable due to the strong subbasal tine situated just above the burr, the well-developed dorsal tine curved toward the anterior, and the straight proximal portion of the beam set obliquely on the burr. The beam between the basal and dorsal tines has a lateral longitudinal groove-like depression and a rib that ranges from the subbasal tine to the dorsal tine. The beam becomes compressed from the sides above the dorsal tine. The dorsal tine may be extremely long (more than 800 mm) and intricately curved, as seen in the specimen from Cava Liberatori (Abbazzi, 1995: pl. 1, fig. 1-2). Although complete mature antlers are not known, antlers from Pietrafitta show a sharp curvature in the area of the primordial posterior tine. The ascending part of the antler is somewhat compressed from the sides and is terminated by a small fork. The middle tine is missing, which may indicate an early ontogenetic stage. Unfortunately, complete mature antlers from Pietrafitta and Forest Bed samples showing the presence of the middle tine are not available. However, the middle tine is found in adult individuals from Rotbav Silvestru, Romania (Fig. A.34 C). Therefore, interpreting some characters is currently difficult.

The skull length of the specimen from Pietrafitta (IGF 4024, cast; MGPF; Fig. A.34 B) measures 470 mm. The frontal bones before the pedicles are slightly concave, and the interfrontal suture has a gently convex profile. The cylindrical pedicles are in a normal position and only slightly compressed from the lateral and medial sides. Each pedicle base is bordered by a weak bony rib from its internal side. The parietal bones are flat. The length of the face is similar to that of deer in the same size group, such as *Cervus*, *Megaloceros*, or *Eucladoceros*. The distance between P^2 and prosthion is more or less equal to the upper tooth row's length. The preorbital fossae are well-developed and deep, and the ethmoidal openings are large. The nasal bones are comparatively long and broad, but they do not extend behind the line connecting the anterior edges of the orbits. The premaxillary bones of the face fragment of the skull from Cava Liberatori (Abbazzi, 1995) have a rather broad anterior part, and the naso-premaxillary suture is long and accounts for 12.5% of the premaxillary bone's total length. The braincase from Salcia (Moldova) is characterized by the bell-shaped basioccipital broadened area of pharyngeal tuberosities.

The lower jaw is relatively tall, with a pronounced angular process and an elevated diastemal region, suggesting that the incisors are positioned above the level of the cheek teeth's grinding surface. However, mandibular pachyostosis is not developed. The mandible fragment RS-7 (ISR) from Rotbav-Silvesrtu shows a short diastema (Radulesco and Samson, 1967), which corresponds to the skull's relatively short distance between P^2 and prosthion.

The P^2 protocone and hypocone are fully separated, creating a cleft on the tooth's lingual side. The P^3 protocone and hypocone are partially separated, resulting in a vertical groove dividing the tooth's lingual wall. The P^2 and P^3 hypocones are supplemented with an internal enamel fold (Azzaroli and Mazza, 1992: fig. 5). The upper molars have a hypoconal enamel fold and a small flat entostyle. Compared to other archaic deer, the lower premolar series is relatively short (the premolar/molar ratio amounts to 60%). The P_4 is molarized, with its metaconid extending anteroposteriorly and its anterior wing joining with the paraconid. In some cases, the entoconid of P_4 also participates in the molarization process and joins with the entostylid.

Distribution. Remains of *P. obscurus* are frequently found in the late Villafranchian deposits of Italy, Romania, Moldova, and the Forest-bed Formation of England. In addition, some sparse remains of *P. obscurus* have been discovered in the late Villafranchian site of Ceyssaguet, France (Croitor and Bonifay, 2001), as well as the Tamanian fauna of Semibalki-1, Azov Region (antler fragment AKM-KP27666), and the Early Pleistocene fauna of Dmanisi, Georgia (Vekua et al., 2010). It is worth noting that some fossils previously assigned to other species should also be attributed to *P. obscurus*. These include the basal fragment of an antler from Tzimbal, Tamanian peninsula, which was reported by Vereschagin (1957) as Megaceros sp., antler fragments from the early Pleistocene of Moldova reported by Alekseeva (1977) as *Eucladoceros* cf. *tetraceros*, and remains from the early Pleistocene site Ubeidiya, Israel, reported by Geraads (1986) as *P. verticornis*. Notably, *P. obscurus* is the only species of the genus that has been recorded in the Near East.

Praemegaceros (*Praemegaceros*) *dawkinsi* (Newton, 1882)

Synonymy:

1872 *Cervus verticornis sp. nov.* (partim): Dawkins, p. 406, fig. 1.
1882 *Cervus dawkinsi sp. nov.*: Newton, p. 145.
1920 *Cervus* (*Praemegaceros*) *Dawkinsi* (Newton): Portis, p. 132.
1956 *Orthogonoceros verticornis* (Dawkins): Kahlke, p. 38.
1961 *Megaceros dawkinsi* (Newton): Azzaroli, p. 6.
1965 *Praemegaceros dawkinsi* (Newton): Kahlke, p. 381.
1979 *Megaceros* (*Megaceroides*) *dawkinsi* (Newton): Azzaroli, p. 7-8.
1994 *Megaceroides dawkinsi* (Newton): Azzaroli, p. 129, figs. 5-6.
1996 *Megaloceros dawkinsi* (Newton): Lister, p. 27.

Nomenclatural acts. In 1872, Dawkins initially identified the antler of a relatively small deer as a juvenile form of *Cervus verticornis*. He provided a brief description of the antler, along with measurements and a figure. Later on, Newton (1882) described this "juvenile" antler as a new species, *Cervus dawkinsi*, and designated the specimen illustrated by Dawkins (1872: fig. 1) as a holotype. Portis (1920) included *C. dawkinsi* in the subgenus *Cervus* (*Praemegaceros*). Kahlke (1956) subsequently designated *C. dawkinsi* as the type species of the genus *Praemegaceros*.

Diagnosis: A deer of medium size. The subbasal tine normally is reduced; in some cases, it may be quite well-expressed (for instance in the type specimen) or present as a vestigial knob. The dorsal tine is reduced; however, it may be present as a vestigial knob as well. The middle and the posterior tines are developed. The antler beam is set obliquely to the burr plane. The beam is straight, without curves in the areas of the dorsal and posterior tines. The antler portion above the posterior tine is shortened. The distal part of the antler is palmed. The pedicles are compressed dorso-ventrally. The cheek teeth are high-crowned.

Holotype: The holotype of this specimen is a shed left antler that belonged to a mature deer of smaller size. The antler exhibits a rather strong cylindrical subbasal tine that is resting on the burr. An evident rib extends from the subbasal tine on the frontal side of the beam, while the dorsal tine is not developed. The middle tine, which is inserted on the anterior side of the beam, is damaged. The next tine represents the first crown branching. The antler beam is set obliquely on the burr, and it is straight with a rounded base. The beam becomes compressed dorso-ventrally in the area of the middle tine. The antler extends into a small palmation, beginning from the first crown tine. The palmation is somewhat concave from the lateral side and convex from the medial side. The main part of the palmation, including the distal tines and the posterior tine, is destroyed.

Locus typicus: Forest-bed, Norfolk, England.

Stratum typicum: Cromer Forest-bed Formation, the middle Pleistocene.

Description. The most complete specimen attributed to this species is the shed left antler M18706, NHML (Fig. A.34 D). The antler beam is set obliquely to the burr and directed sideways at an angle of about 45-50º. A rudimentary cone-shaped subbasal tine is located close to the burr, while the dorsal tine is missing. The middle tine is well-developed and compressed dorsoventrally, with its distal portion somewhat bent upward and inward. Its length is 180.0 mm. The posterior tine is also developed, and the distance between the antler burr and the posterior branch is 280.0 mm. The beam becomes increasingly compressed in the dorsoventral direction towards the distal end and terminates in a palmation, with only one crown tine preserved. The preserved crown tine is rather straight and compressed from the sides, with a length of 220.0 mm. The distal portion of the antler palmation is destroyed, and the transversal section of the palmation is irregular, with the anterior part being thicker (35.7 mm) than the posterior part (15.0 mm). A groove-like depression bordered by a rib extends from the basal rudimentary tine to the middle tine. The beam is straight and does not form an angle in the area of the posterior tine.

In contrast, the antler M18168 (NHML) lacks the vestigial subbasal tine, but a reduced small dorsal tine is present in the medial position on the beam. The distance between the second tine and burr is 53.5 mm. The vestigial tine is asymmetrical, with its top pointing towards the anterior. The pedicle is short, robust, compressed dorso-ventrally and proportionally is excessively robust if compared to the antler base. The circumference of the antler base amounts to 17.5 cm, while the pedicle circumference amounts to 20 cm.

The shed left antler M6358 (NHML) maintains both the knob-like vestigial subbasal tine on the anterior side close to the burr and the vestige of the dorsal tine on the upper side of the beam. The individual variation of antler morphology concerns the degree of reduction of basal tines. The subbasal tine is developed in the type specimen. However, it normally is missing or represented as a knob-like vestige. The sample of eight available specimens shows the subbasal tine maintained as a small button in three specimens of *P. dawkinsi* only. Five specimens lack the subbasal tine rudiment. The rudiment of dorsal tine is present in three specimens only. Four antlers (50% of the sample stored in NHML) lack any vestiges of proximal tines.

According to Azzaroli (1953), dentition is characterised by smaller dimensions than that of *P. verticornis*. The cheek teeth are mesodont, with comparatively thick enamel. The strong basal columns are developed in lower molars. P_4 is primitive. The lower premolar series is relatively long; the premolar/molar series length ratio amounts to 65.5%. Azzaroli (1953) reports a pachyostosis of the lower mandible in *P. dawkinsi*, however, the mandibles seem to have the normal shape (the mandible thickness below M_2/M_3 is 26.5 – 24.4 mm). The body mass estimation based on mandibles ascribed by Azzaroli (1953) to this species amount ca. 220 kg. The sideward orientation of palmated antlers and the shape of pedicles suggest that the evolution of *P. dawkinsi* passed through the stage of a giant form with large heavy antlers.

Distribution. The remains of *P. dawkins*i are known only from the Middle Pleistocene of England.

Praemegaceros (*Praemegaceros*) *mosbachensis* (Soergel, 1927)

Synonymy:

1927 *Cervus* (*Megaceros*) *mosbachensis* sp. nov.: Soergel, p. 375.
1953 *Megaceros mosbachensis* (Soergel, 1927): Azzaroli, p. 51.
1956 *Praemegaceros verticornis* (Dawkins, 1872): Kahlke, p. 30.
1967 *Praemegaceros mosbachensis* (Soergel, 1927): Radulesco and Samson, p. 321.
1990 *Praemegaceros (Praemegaceros) mosbachensis* (Soergel, 1927): Vislobokova, p. 160.

Nomenclatural acts. Reynolds (1929) and Radulesco and Samson (1967) suggested that the antlers of *Cervus* (*Megaceros*) *mosbachensis* Soergel, 1927 share a morphological affinity with *P. dawkinsi*. The deer from Mosbach shows similarity to *P. obscurus*, but some details in antler morphology indicate a somewhat more advanced form. Azzaroli (1953) included *P. mosbachensis* in his informal "*verticornis*" group. Vislobokova (1990) considered *Megaceros mosbachensis* as a senior synonym of *Allocaenelaphus arambourgi* Radulesco and Samson, 1967. Later, Vislobokova (2013) adopted Kahlke's (1956) viewpoint and included *P. mosbachensis* in the synonymy of *P. verticornis*, admitting an extensive individual variation in antler morphology for this deer. I previously proposed considering *Megaceros mosbachensis* as a nomen oblitum (Croitor, 2005), but now I believe that this species name should be maintained since it represents a transitional evolutionary stage between *P. obscurus* and *P. dawkinsi*.

Diagnosis: The species can be distinguished by its large size, highly divergent antlers, and prominent subbasal tine. The antlers exhibit a broad flattening that extends from the middle tine towards the distal end of the antler.

Holotype: the antlered braincase figured in Soergel (1927: tab 17, figs. 5-8).

Locus typicus: Mosbach, Germany.

Stratum typicum: lower level of Mosbach sands.

Description. The deer from Mosbach is closely related to *P. obscurus* but exhibits more advanced antler morphology, primarily due to the strongly expressed antler flattening above the middle tine. The dorsal tine in the type specimen is present on the right antler only and may be disappearing. *P. mosbachensis* cannot be considered a synonym of *P. verticornis*, as certain antler morphology details suggest that these two cervid forms belong to different phyletic lineages. *P. mosbachensis* retains the well-developed subbasal tine, whereas the lineage of *P. verticornis* lost this feature during the evolutionary transition from *P. pliotarandoides* to *P. verticornis*. The antler beam in *P. mosbachensis* becomes flattened in the area of the middle tine, whereas *P. verticornis* always exhibits a cylinder-shaped beam, even in forms that have evolved distal palmations. Thus, the antlered skull from Pakefield displays this characteristic (Harmer, 1899). Soergel (1927) also described another antler specimen from the same level of the Mosbach sands, which is characterized by a vestigial state of both subbasal and dorsal tines, and thus reminiscent of the typical morphology of *P. dawkinsi*, according to Radulesco and Samson (1967).

Distribution: the Middle Pleistocene of Western Europe.

Subgenus *Nesoleipoceros* Radulesco and Samson, 1967

Nomenclatural acts: Radulesco and Samson (1967) established the genus *Nesoleipoceros* for the "dwarfed insular megacerines" found in Corsica, Sardinia, Sicily, and Crete: *N. cazioti*, *N. algarensis*, *N. messinae*, and *N. cretensis*, respectively. They also suggested that *Allocaenelaphus arambourgi* Radulesco and Samson (= *Praemegaceros obscurus*), a primitive megacerine deer from Eastern Europe, might be a possible ancestor of all Mediterranean dwarfed species. However, Caloi and Malatesta (1974) disputed this claim, stating that the antler morphology of the Sardinian deer does not match that of *Allocaenelaphus* and a direct phyletic relationship seems unlikely. They further restricted the genus *Nesoleipoceros* to the type species *N. cazioti*, and Azzaroli (1979) concurred that the genus is polyphyletic. Croitor et al. (2006) reclassified *Nesoleipoceros* as a subgenus of *Praemegaceros* and included the continental giant *P.* (*N.*) *solilhacus* in this subgenus because of its similar antler shape to the type species *P.* (*N.*) *cazioti*.

Diagnosis: Deer of medium or very large size. The proximal portion of the antler beam is cylindrical; the distal portion of the antler is compressed mediolaterally and normally is extended into a palmation. The antler beam does not form a sharp curvature in the area of the posterior tine. The basal tine occasionally may be present, quite small, straight, and inserted on the lateral side of the beam. Often this tine is represented by a knob-like vestige. The dorsal tine is missing. The middle tine is well developed, compressed dorso-ventrally and may form a small palmation. The posterior tine is normally present in the fully-grown antlers. The crown tines are inserted on the anterior and posterior sides of the beam; the posterior tines normally form a palmation of variable size and shape. The lower fourth premolar normally is not molarised or is occasionally fully molarised.

Differential diagnosis: Unlike the subgenera *Orthogonoceros* and *Praemegaceros*, the antlers of *Nesoleipoceros* do have not a dorsal tine situated on the upper side of the beam; the beam does not form a sharp curvature in the area of the posterior tine. P_4 generally is more primitive if compared to the deer of the subgenera *Orthogonoceros* and *Praemegaceros*.

Comment: the basal tine of *Nesoleipoceros* antler are not homologous with those of the subgenera *Praemegaceros* and *Orthogonoceros*. Possibly, the lineage of *Nesoleipoceros* represents a genuine genus, which is quite distant from *Praemegaceros*.

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

Other species: *P. solilhacus* (Robert, 1830), *P. sardus* (van der Made and Palombo, 2005).

Praemegaceros (*Nesoleipoceros*) *cazioti* (Depéret, 1897)

Synonymy:

1897 *Cervus* (*Eucladoceros*) *cazioti* sp. nov.: Depéret, p. 115, pl. 2, figs 1, 2-2a.
1955 *Megaceros* (*Anoglochis*) *cretensis* (Simonelli): Comaschi Caria, 17, pl. 4-5.
1956 *Cervus algarensis sp. nov.*: Comaschi Caria, p. 1, tab. 1.
1957 *Orthogonoceros verticornis* (Dawkins): Comaschi Caria: p. 5.
1960 *Cervus Cazioti* (Depéret, 1897): Sigogneau: p. 62.
1961 *Megaceros cazioti* (Depéret, 1897): Azzaroli p. 13, tab. 7, fig. 9-9a, tab. 9, fig. 5.
1961 *Megaceros algarensis* (Comaschi Caria, 1956): Azzaroli, p. 14, pl. 8, fig. 3.
1967 *Nesoleipoceros cazioti* (Depéret, 1897): Radulesco and Samson, p. 334.
1967 *Nesoleipoceros algarensis* (Comaschi Caria, 1956): Radulesco and Samson, p. 334.
1974 *Megaceros* (*Nesoleipoceros*) *cazioti* (Depéret, 1897), Caloi and Malatesta, p. 165.
1981 *Megaceroides* (*Nesoleipoceros*) *cazioti* (Depéret, 1897): Caloi et al., p. 34.
1981 *Praemegaceros* (*Nesoleipoceros*) *cazioti* (Depéret, 1897): Vislobokova, p. 160.

Nomenclatural acts. The original description of the species is based on a shed left antler (Depéret, 1897: tab. 2, fig. 1) and a complete lower tooth row (ibidem, p. 116, tab. 2, fig. 2-2a) found at the Nonza site in North Corsica. However, the species description does not provide a formal diagnosis and a type designation. *P. cazioti* was considered an archaic representative of the subgenus Eucladoceros due to the primitive morphology of its premolars and the flattened antlers (Depéret, 1897). According to Azzaroli (1961), the dentition and antler morphology of the Corsican deer is similar to that of the mainland giant deer and particularly to another stunted megacerine form *Megaceros dawkinsi* (= *Praemegaceros dawkinsi*) from the Middle Pleistocene of England. Azzaroli included the Corsican deer in the arbitrary "*verticornis* group" of the genus *Megaceros* Owen and pointed out its possible relationship to the mainland large-sized deer *M. verticornis* (= *Praemegaceros verticornis*). Later, Radulescu and Samson (1967) designated *Cervus cazioti* as the type species of the new genus *Nesoleipoceros*, which also included the Mediterranean island species. Caloi and Malatesta (1974) included the species name *Cervus algarensis* Comaschi Caria in the synonymy of *P.* (*N.*) *cazioti*. However, Azzaroli (1979) did not accept the placement of all late Pleistocene megacerines from Corsica and Sardinia into a single species.

Palombo (1986) proposed that *P.* (*Nesoleipoceros*) *cazioti* (= *Megaceros* [s. l.] *cazioti*: Palombo, 1986, p. 206) may be divided into several subspecies, including *M.* (s. l.) *cazioti* algarensis from Dragonara and other locations in Sardinia, *M.* (s. l.) *cazioti* ssp. from Porto Vesme (Sardinia), a smaller subspecies from Corsica, and an unidentified species *Megaceros* (s. l.) sp. from Capo Figari. Petronio (1990) proposed three subspecies within *P.* (*Nesoleipoceros*) *cazioti*: the comparatively large *P. cazioti algarensis* from Sardinia, another smaller subspecies *P. cazioti* ssp. from Sardinia, and the nominal subspecies *P. cazioti cazioti* from Corsica. However, no definite conclusion was made regarding the subspecific division of *P.* (*Nesoleipoceros*) *cazioti*.

Diagnosis: A medium-sized species slightly larger than fallow deer. The antler beam is compressed dorso-ventrally in its proximal part, and compressed mediolaterally in the distal part. The subbasal and dorsal tines are absent. The basal tine is straight and sharp, situated on the lateral side of the beam and pointed anteriorly. The middle tine is compressed dorso-ventrally, and the position of the posterior tine may be variable relative to the middle tine. The middle portion of the antler has large, flat posterior crown tines that may form a small palmation. The distal part of the antler may have small ramifications situated on the anterior and posterior sides of the beam. The burr is set obliquely to the beam. The pedicles are slightly compressed dorso-ventrally. The cranial morphology is not paedomorphic and maintains normal proportions for a medium-sized deer. The nasal bones do not extend beyond the line connecting the anterior edges of the orbits. The ethmoidal openings are normally developed but may be reduced in some cases. The preorbital fossae are reduced. The premaxillary bones are broad and square-shaped. The diastema of the lower mandible is shorter than the length of the lower molar series. The fourth lower premolar is not molarized.

Syntypes. The antler beam figured in Depéret's (1897) paper has a rounded base and is set very obliquely on the burr, becoming flat just above it. The basal tine is inserted 80 mm above the burr, strongly compressed dorso-ventrally, and set at right angles on the anterior side of the beam. The tip of the tine is broken off. The middle tine is located 80 mm further from the basal tine, also compressed dorso-ventrally, and set on the anterior side of the beam at right angles. The beam becomes quite flat above the middle tine. The antler described by Depéret was not identified among the original material stored in PMUL.

The left hemimandible fragment FSL17970 (PMUL), with a complete tooth row, is believed to belong to the same individual as the antler described by Depéret (1897). It is characterized by rather high-crowned cheek teeth, and M_3 is shortened due to its reduced third lobe. P_4 is simple. The length of the lower dentition is 108.5 mm, and the premolar series is relatively long (premolar/molar series length ratio is 60.5%).

Locus typicus: Nonza, Corsica.

Stratum typicum: the Late Pleistocene of Nonza.

Description. This species is slightly larger than the modern fallow deer. The burr is set obliquely to the beam. The antler beam is compressed dorsoventrally in the proximal part and compressed lateromedially in the distal part. The subbasal and dorsal tines are missing, while the basal tine is straight, sharp, and positioned on the lateral side of the beam, pointing towards the anterior. The middle tine is compressed dorsoventrally. A small palmation of variable size is developed on the posterior side of the third quarter of the beam, with several prongs and digitations occurring on the palmation's edge. The most distal part of the antler is also flat but is not palmated. The terminal part of the antler has several small crown tines on its anterior and posterior sides,

The cranial morphology of this species maintains the normal proportions for a deer of its body size, and is not "paedomorphic" (Croitor et al., 2006). The frontal bones are flat with a depressed sagittal profile between the orbits, and the supraorbital openings are very large. The pedicles are short, slightly compressed anteroposteriorly, moderately divergent, and sloped caudally. The face length is approximately half the total skull length in mainland deer of similar size, such as *Dama dama* and *Axis axis*, and is only slightly shorter than the face length in *P. obscurus* and *E. senezensis*. The anterior edge of the orbit is situated above M^3, which may be correlated with the relatively large tooth row length. The basioccipital has a bell-shaped structure with a broadened area of pharyngeal tuberosities. The nasal bones do not extend behind the line connecting the anterior edges of the orbits. The ethmoidal openings are normally developed, although they may be reduced in some cases. The premaxillary bones are broad and square-shaped. The mandibular pachyostosis is not developed (Croitor et al., 2006). The general shape of the skull is similar to that of Eucladoceros, but the face morphology and masticatory apparatus exhibit some peculiar characteristics resulting from extreme adaptation to grazing, which is particularly advanced in *P. cazioti* from the late Würm site of Dragonara, Sardinia (Caloi and Malatesta, 1974). Unlike *Eucladoceros*, the upper molars of this species never possess a protoconal fold. The lingual wall of P^2 is not cleft or segmented by a vertical groove, meaning the protocone and hypocone are not separated. The lingual wall of P^3 is not grooved. The hypocone in both P^2 and P^3 is supplemented with an internal enamel fold. The upper molars have a small entostyle and a hypoconal enamel fold, which may be absent. P_4 is never molarised. The metapodials of this species are very thin. At least two chronosubspecies have been identified.

Subspecies:

Praemegaceros (*Nesoleipoceros*) *cazioti algarensis* Comaschi Caria, 1956

Synonymy:

1956 *Cervus algarensis sp. nov.*: Comaschi Caria, p. 1, tab. 1.
1961 *Megaceros algarensis* (Comaschi Caria, 1956): Azzaroli, p. 14, pl. 8, fig. 3.
1967 *Nesoleipoceros algarensis* (Comaschi Caria, 1956): Radulesco and Samson, p. 334.

Diagnosis. The body size of this subspecies is comparatively larger than that of the nominotypical subspecies. The cheek teeth are large and mesodont. The upper cheek tooth row is relatively long, accounting for approximately one-third of the skull's condylobasal length. The lower premolar series is also comparatively long, with a ratio between premolar and molar series higher than 60%. The diastema is shorter than half of the lower dentition length, and the area of *musculus masseter* insertion is larger, extending toward the anterior up to the M_3 level on the lower mandible and up to the P^4 level on the skull. The metapodials are also relatively longer.

Holotype: a left complete antler (Comaschi Caria, 1956: p. 1, tab. 1; Azzaroli, 1961: tab. VIII, fig. 3).

Locus typicus: Alghero (Sardinia).

Stratum typicum: Late Pleistocene, late Würmian epoch.

Description. This subspecies is a specialized grazing form characterized by its larger body size. The upper cheek teeth are large, with the upper tooth row accounting for one-third of the condylobasal skull length, and mesodontous in shape. The premolar series is relatively long, with the premolar/molar length ratio ranging between 62.7% and 64.5%. The diastema of the lower mandible is shorter than half the length of the lower tooth row. The area of *musculus masseter* insertion on the lower mandible is larger and extends anteriorly to the M_3 level. The preorbital fossae are reduced compared to other subspecies (Croitor et al., 2006).

Distribution: the Late Pleistocene of Sardinia.

Praemegaceros (*Nesoleipoceros*) *cazioti cazioti* (Depéret, 1897)

Diagnosis: This subspecies has a body size that is similar to modern fallow deer. The upper cheek tooth-row is relatively short, measuring below 30% of the condylobasal skull length. The series of lower premolars is also relatively short, with a ratio between lower premolar and molar series often below 60%. The diastema of the lower mandible is longer than 1/2 of the lower tooth row length, and the masseter area on the lower mandible does not reach the level of M_3. The preorbital fossae are normally developed, and the ethmoidal openings have varied sizes, with some cases of reduction. The area of *musculus masseter* insertion is smaller and does not extend towards the anterior beyond the P^4 level on the skull.

Syntypes: the series includes a basal fragment of the left antler (Depéret, 1897: tab. 2, fig. 1), which was not identified among the original materials stored in the Paleontological Museum at the University of Lyon. Additionally, a fragment of the left hemimandible with a complete tooth row, FSL17970, is also considered a syntype and is housed at the Paleontological Museum at the University of Lyon (Depéret, 1897: tab. 2, fig. 2-2a; Pereira, 2000: p. 446, fig. 8). According to Depéret (1897), these remains likely belonged to the same individual.

Locus typicus: the Cave Margine-Sud, South from Nonza, Haute-Corse, Corsica.

Stratum typicum: Upper Pleistocene, early Würmian epoch (80.000-100.000 y. BC).

Description. This subspecies is characterized by a smaller body size and a lower degree of specialization. The teeth are smaller and brachydont. The relative length of the upper tooth row is below 30% of the condylobasal skull length, and the diastema is longer than 1/2 of the lower tooth row length. The lower premolar series is relatively short, and the ratio between lower premolar and molar series is often below 60%. The area of *musculus masseter* insertion on the lower mandible is reduced and does not reach the level of M_3. The preorbital fossae are normally developed (Croitor et al., 2006).

Distribution: Riss-Würm sites Maccinaggio and Coscia (Corsica).

Praemegaceros (*Nesoleipoceros*) *sardus* (van der Made and Palombo, 2005)

Synonymy:

2005 *Megaloceros sardus* sp. nov.: van der Made and Palombo, p. 165, pls. 1-4.

Holotype: a right metacarpal (van der Made and Palombo, 2005: pl. 4, fig. 1).

Locus typicus: Santa Lucia 1, Southwestern Sardinia.

Stratum typicum: the Middle Pleistocene deposits (ca. 450 ka) of the Canta Lucia quarry.

Emended diagnosis: This is a medium-sized deer with robust metapodials and phalanxes. The linear measurements are 25-40% larger than those of the genotype species. P_4 is not molarized, and the upper cheek teeth lack supplementary enamel folds. The relative length of the lower premolar series is very long, measuring 67.1% of the total tooth row length.

Description. The species is considered a larger and less specialized ancestor of *P.* (*N.*) *cazioti*. Compared to the disproportionally thin metacarpals of *P.* (*N.*) *cazioti*, the metacarpals of

P. (*N.*) *sardus* are quite robust, indicating a lower degree of specialization of the former species to insular conditions (van der Made and Palombo, 2005). The length of the lower dentition of the mandible shown in Plate 2 (van der Made and Palombo, 2005) is 119 mm (measured from the photo), falling within the size range of *P.* (*N.*) *cazioti* from Dragonara (L = 107.1 – 120.1 mm, n = 4), but with a very long premolar series (67.1% of molar series length), representing a specific direction of evolutionary specialization of the insular lineage of *Nesoleipoceros* (Croitor et al., 2006). The size of dentition in *P.* (*N.*) *sardus* is still relatively smaller than in *P.* (*N.*) *cazioti*, but the dentition morphology already shows a high degree of evolutionary modification, with thick dental enamel, loss of additional dental enamel folds, and relatively high tooth crowns.

Distribution: the Middle Pleistocene of Sardinia.

Praemegaceros (*Nesoleipoceros*) sp. from Su Fossu

Another insular form of *Nesoleipoceros*, which is even larger and older (>450 ka), has been reported from the Su Fossu de Cannas Cave in Sardinia (Melis et al., 2016). Its size and age suggest that it is an earlier ancestor of the *Nesoleipoceros* species previously found on the island, such as *P.* (*N.*) *sardus* and *P.* (*N.*) *cazioti*.

Praemegaceros (*Nesoleipoceros*) *rossii* (Pereira, 2001)

Synonymy:

2001 *Cervus elaphus rossii* ssp. nov.: Pereira, p. 199, pls. 1, 2.

Locus typicus: Castiglione Cave (Corsica)

Stratum typicum: the Middle Pleistocene sediments of Castiglione Cave

Description. This deer is highly similar to either *P. sardus* or the unnamed deer from Su Fossu. The morphology of upper and lower teeth, as illustrated by Pereira (2001), is very similar to that of *P. sardus*, but slightly larger. Additionally, the limb bones of the deer from Castiglione are relatively robust (Pereira, 2001). Despite the limited number of remains, there is no doubt that the Castiglione cervid belongs to the *P. sardus* – *P. cazioti* lineage.

Praemegaceros (*Nesoleipoceros*) *solilhacus* (Robert, 1830)

Synonymy:

1830 *Cervus* (*Anoglokis*) *solilhacus sp. nov.*: Robert, p. 77, pl. II, fig. 1.
1886 *Cervus* (*Dama*) *priscus sp. nov.*: Moullade, p. 304, fig. 1.
1957 *Tamanalces caucasicus sp. et gen. nov.*: Vereschagin, p. 55, fig. 20.
1965 *Praemegaceros sp.*: Kahlke, p. 389, fig.7.
1967 *Praemegaceros solilhacus* (Robert): Radulesco and Samson, p.323.
1979 *Megaceros* (*Megaceroides*) *solilhacus* (Robert): Azzaroli, p. 8.
1979 *Megaceros solilhacus* (Robert): Caloi and Palombo, p. 129-136.
1993 *Megaceroides solilhacus* (Robert): Azzaroli and Mazza, p. 9.

Nomenclatural acts. In 1830, Robert reported finding two partial skeletons of large deer in the Polignac area (Haute-Loire), which he identified as new species: *Cervus* (*Anaglokis*) solilhacus and *Dama* (*Catoglokis*) *polignacus*. *Cervus solilhacus* had a high insertion of the first tine and a compressed antler beam in its distal portion above the tine. The individual assigned to *Dama polignacus* was rather old, as suggested by the advanced wear of its upper dentition, and approached the size of an elk. Robert noted that the main distinguishing characteristic between the two species, besides the shape of palmation and morphological details of postcranial bones, was a strong basal tine right above the antler burr. Robert did not figure the antlers of the second deer because they were badly damaged. Additionally, Robert reported remains of a significantly smaller deer from the same area interpreted as a juvenile form of *Dama polignacus*. Azzaroli (1979) revised Robert's material and ascribed all the fossil deer remains from Soleilhac to the species *Megaceros* (*Megaceroides*) *solilhacus*, choosing a proximal fragment of an antler with a pedicle as a lectotype. Moullade (1886) established one more species from the vicinity of Soleilhac, *Cervus* (*Dama*) *priscus*, based on a well-preserved complete palmed antler. Azzaroli (1979) included this species in the synonymy of *P. solilhacus*. The collection of fossils from Soleilhac (Crozatier Museum) represents a set of specimens with different geological ages found on the extensive area of a riverbank (Bonifay, 1986), and the revision of cervid fossils from Soleilhac revealed the presence of several species in the sample. The fossils ascribed by Robert to the juvenile individual of *D. polignacus* most likely belong to *D. clactoniana*. The large size and the presence of a strong basal tine on the antler of the "old individual" of *D. polignacus* suggest that it is more likely to belong to *P. obscurus*.

Diagnosis: This species exhibits a very large body size and heavy antlers. The antler beam is obliquely set on the burr and extends into a broad palmation with a sharp tip and small digitations on the posterior side. The anterior crown tines are typically undeveloped. The subbasal tine may be reduced or occasionally present as a vestigial button. The basal tine is straight and sharp, inserted on the anterior side of the beam at a long distance from the burr, while the middle tine is flat and extended into a small palmation with small prongs on the margins. Unlike *P. verticornis*, the proximal tine situated on the dorsal side of the beam is absent, and the antler beam is not bent in the area of the posterior tine. The pedicles are massive, compressed dorsoventrally, and sloped backward and sideward. This species does not exhibit mandibular pachyostosis, and the lower jaw maintains normal proportions. The diastema is longer than the lower molar series, and the lower fourth premolar (P_4) is not fully molarized.

Neotype: the left antler of 2003-4-346-SOL (MCP), originally designated as lectotype by Azzaroli (1979: p. 8, tab. IV, fig. 1-1a), is missing its distal part just above the posterior tine. This proximal portion is currently housed in the Musée Crozatier, Le Puy under the collection number 2003-4-346-Sol.

Locus typicus: Soleilhac (Central French Massif).

Stratum typicum: early Middle Pleistocene.

Description. The neotype's pedicle is compressed dorsoventrally, similar to *P. verticornis* and *P. dawkinsi*. Its maximum diameter is 79.0 mm, and the maximum diameter of the burr is 101.0 mm. The antler beam is obliquely set on the burr and directed somewhat sideward. The antler base is oval and compressed dorsoventrally, lacking basal tines or their vestiges. The beam becomes notably flat at the middle tine, located 215 mm from the burr, bending slightly toward the posterior. It curves gently toward the anterior at the posterior tine, and a groove-like longitudinal depression runs on the anterior side of the beam from the middle tine to the burr. The complete left antler 2003-4-397-SOL (MCP) of *P. solilhacus* shares a remarkable resemblance in shape to *P. cazioti*, suggesting a close phylogenetic relationship between the two species (Fig. A.35). The antler has a straight length of 1300 mm, a pedicle diameter of 79.0 mm, and an antler base diameter of 84.0 mm. The proximal part of the antler bears a long, straight basal tine, which is missing in the lectotype. The development of the basal tine seems to be a variable character in this species, as it is preserved as a vestigial knob in the shed antler from the Tiraspolian gravel (Croitor et al., 2006).

The distal palmed portion of the antler is gently curved and elevated, but it does not form a sharp curvature as in *P. verticornis* and *P. pliotarandoides*. Just above the posterior tine, the antler extends into a large palmation with a leaf-like shape and small digitations on its posterior edge. The anterior part of the palmation has a single sharpened prong, and the middle tine is terminated with a small palmation with digitations. Unlike *P. verticornis* and *P. obscurus*, *P.* (*N.*) *solilhacus* does not have a dorsal tine. The antler bauplan of *P.* (*N.*) *solilhacus* is very different, as the distal palmation appears to be derived from posterior crown ramifications (Vislobokova, 2012). The morphology of the antler palmation, including the specific character of a distal sharp prong, resembles that of *Sinomegaceros*. However, in contrast to *Sinomegaceros*, both *P.* (*N.*) *solilhacus* and *P.* (*N.*) *cazioti* have a well-developed middle tine. We have limited knowledge about the cranial morphology of *P.* (*N.*) *solilhacus*. Its frontal bones are flat and only slightly depressed before the pedicles.

The tooth row length of the mandible 2003-4-439-SOL (sin, MCP) (Azzaroli, 1979: pl. 3, fig. 3-3a) is 156.3 mm, and the premolar/molar series length ratio is 62%. The mandibular body is comparatively high, and the diastema is moderately long, slightly longer than the lower molar series, and attains 65.6% of the lower dentition length. P_4 is variable in morphology but is often not fully molarized. The lower molars are supplemented with ectostylids, and mandibular pachyostosis is not developed. The upper cheek tooth row 2003-4-421-SOL (*sin*, MCP) possibly corresponds to the upper maxilla figured by Robert (1830: pl. II, fig. 4). The upper molars and premolars have weak cingulum-like basal structures, and the lingual side of P^2 is divided by a vertical groove. This character distinguishes *P.* (*N.*) *solilhacus* from *P.* (*N.*) *caziotі*. The hypocone of premolars is supplemented with an additional interior enamel fold, and the upper molars are characterized by an enamel fold in the posterior wing of the hypocone. The M^1 and M^2 have an additional enamel fold on the anterior wing of the hypocone, while the enamel of the posterior wing of the protocone is undulated.

Distribution. The remains of *P. solilhacus* were reported from the early Middle Pleistocene faunas of France, Germany, Italy, South Russia and Moldova (Azzaroli and Mazza, 1993; Croitor et al., 2006). *P. solilhacus* became extinct by the end of the Mindel glaciation.

Subgenus *Orthogonoceros* Kahlke, 1956

Type species: *Cervus verticornis* Dawkins, 1872.

Other species: *Praemegaceros pliotarandoides* (De Alessandri, 1903).

Diagnosis. Deer of very large body size. The pedicles are compressed in the anteroposterior direction, divergent, and slope backward. The frontal bones are flat, and the braincase is short and relatively broad. The antler beam is cylindrical, with the basal part set at a right angle to the burr plane. The beam bends sideward in the area of the dorsal tine and then abruptly upward in the posterior tine region. The subbasal tine is either a small vestige or completely absent. The cylindrical dorsal tine is inserted on the upper side of the beam and curves anteriorly. The posterior tine is typically present in fully-grown antlers. The crown tines are oriented in the parasagittal plane. P_4 is usually molarized. Antler beam is not obliquely set to the burr, distinguishing *Orthogonoceros* from the subgenera *Nesoleipoceros* and *Praemegaceros*.

Distribution: the Middle Pleistocene of Europe.

Praemegaceros (*Orthogonoceros*) *pliotarandoides* (De Alessandri, 1903)

Synonymy:

1903 *Cervus pliotarandoides* sp. nov.: De Alessandri: p. 11, fig. 4-5.
1920 *Cervus* (*Praerangifer*) *pliotarandoides* (De Alessandri, 1903): Portis, p. 137.
1948 *Cervus cf. pliotarandoides* (De Alessandri, 1903): Gromov, p. 53.
1959 *Eucladoceros pliotarandoides* (De Alessandri, 1903): Verestchagin, p. 60-62, fig. 30.
1967 *Psekupsoceros orientalis* gen. nov. sp. nov.: Radulesco and Samson, p. 332, fig. 5.
1967 *Orthogonoceros verticornis* (Dawkins, 1872): Melentis, p. 79, fig. 2 pl. 1-2.
1976 *Megaceros verticornis* (Dawkins, 1872): Azzaroli, p. 485, pl. 1-2.
1979 *Megaceros* (*Megaceroides*) *verticornis dendrocerus* (Ambrosetti): Azzaroli, p. 7.
1990 *Eucladoceros orientalis* (Radulesco and Samson, 1967): Vislobokova, p. 158.
1993 *Megaceroides orientalis* (Radulesco and Samson, 1967): Azzaroli and Mazza, p. 6, fig. 3.
2004 *Praemegaceros pliotarandoides* (De Alessandri, 1903): Croitor and Kostopoulos, p. 155, fig. 15.
2013 *Eucladoceros orientalis pliotarandoides* (De Alessandri, 1903): Bajgusheva and Titov, p. 116, figs. 4, 5.

Nomenclatural acts. De Alessandri (1903: p. 11, fig. 4-5) proposed the new species name Cervus pliotarandoides for the left shed antler from the "Villafranchian" of Cortiglione Monferrato and suggested that the new species was closely related to modern Rangifer. The description was accompanied by a figure and measurements of the antler, but a formal species definition and type designation were not provided. Portis (1920) included *C. pliotarandoides* in the subgenus *Cervus* (*Praerangifer*), but this subgeneric name is now considered nomen oblitum. Kahlke (1956) and Azzaroli (1976, 1979) believed that *C. pliotarandoides* represented an individual variation of *P. verticornis* and included it in the synonymy of the latter species.

Radulescu and Samson (1967) established the new species and genus *Psekupsoceros orientalis* from the Psekups-Saratovskaya site, North Caucasus. Although the Romanian authors mentioned a strong similarity between *P. orientalis* and *C. pliotarandoides*, they concluded that *P. orientalis* was distinguished by the absence of a subbasal rudimentary tine, the orientation of the first tine, and the supposed structure of the distal part of the antler. The unsatisfactory state of the *Psekupsoceros orientalis* holotype did not allow Radulescu and Samson (1967) to make a correct conclusion on the systematic position of this deer.

Bajgusheva (1994) mentioned the presence of an additional rudimentary subbasal tine in the type antler from Psekups-Saratovskaya, which was, however, destroyed and never restored later. This additional subbasal tine is the same as the small tine found right above the burr in *Cervus pliotarandoides*, and as mentioned above, the absence of this tine in the specimen from Psekups-Saratovskaya was considered by the Romanian authors as one of the distinguishing characteristics. The dorsal tine in the Psekupsan deer is most likely wrongly restored. However, in the antler of *P. orientalis* from Mariupol (Ukraine), which was also mentioned by Radulescu and Samson (1967), this tine is situated on the medial side of the beam and curved outward, as in the type specimen of *C. pliotarandoides*. Based on these observations, Croitor and Kostopoulos (2004) concluded that *Psekupsoceros orientalis* Radulescu and Samson is a junior synonym of *Praemegaceros pliotarandoides* (De Alessandri).

Diagnosis. The species is of very large body size. The antlers are present with a proximal portion featuring a frequently present small vestigial subbasal tine (which may be absent), a rather short cylindrical dorsal tine, and a posterior tine. The middle tine is absent. The antler beam typically bends sideward in the area of the dorsal tine and turns upright in the area of the posterior tine. The distal portion of the antler beam above the posterior tine dichotomously branches, and each branch terminates in a dichotomous bifurcation, therefore the antler terminates in four crown tines. The pedicles are cylindrical in shape. The upper molars lack a protoconal fold or hypoconal spur. The lingual wall of P^2 is not cleft, and the inner wall of the premolar hypocone is undulated. P_4 is molarized.

Holotype. The left shed antler is characterized by a vertical position of the antler base on the burr, a weak subbasal tine, a dorsal tine located on the medial side of the beam and curved towards the anterior, and a short, hook-like posterior tine. The crown bifurcation has been destroyed. The antler beam is cylindrical, gently curved backwards in the area of the dorsal tine, and sharply turned upright in the area of the posterior tine (De Alessandri, 1903: p. 11, fig. 4-5). The original specimen is currently held at the Geological Museum of Turin.

Locus typicus: Cortiglione Monferrato (North Italy).

Stratum typicum: Galerian, late Early Pleistocene.

Description. This species achieved a body mass of approximately 400 kg and developed relatively simple antlers with advanced reduction of proximal tines, a characteristic that distinguishes it from *P. obscurus*. The subbasal tine is typically small and may be reduced until the stage of a knob-like vestige. The curved, cylinder-shaped dorsal tine is directed towards the anterior and is relatively short, whereas the posterior tine is strong and hook-like. The middle tine is typically not developed.

The holotype lacks its distal portion, but fine, complete antlers discovered in Eastern and Southeastern Europe exhibit a stable shape of the crown portion. Specifically, the beam above the posterior tine is dichotomously branched, with each branch terminating in a dichotomous bifurcation. As a result, the total number of main crown tines is four, although supplementary prongs on the antler crown may occur. Furthermore, the antler crown is oriented in the parasagittal plane (Melentis, 1967; Radulesco and Samson, 1967; Baygusheva, 1994; Croitor and Kostopoulos, 2004).

Kahlke (1956) and Azzaroli (1976, 1979) proposed that *C. pliotarandoides* De Alessandri represents a variant of *P. verticornis* and thus included it in the synonymy of the latter species. Nevertheless, *P. pliotarandoides* differs from *P. verticornis* in the absence of the medial tine and the frequent presence of a subbasal rudimentary tine located directly above the burr. Radulesco and Samson (1967) observed that the vestigial subbasal tine is absent in the majority (76.29%) of *P. verticornis* specimens from Süßenborn. Only a knob-like rudiment is observable in 21.65% of specimens, while a clearly expressed subbasal tine is recorded in only 2.06% of specimens. This less evolved variant of the verticornis lineage is found only in older Early Pleistocene faunas, characterized by the absence of red deer *Cervus elaphus*.

The Russian authors traditionally classify De Alessandri's deer as *Eucladoceros pliotarandoides*, apparently because of the dichotomously branched crown tines that resemble the crown tines of *E. dicranios* (Verestchagin, 1959; Flerov, 1962; Alekseeva, 1977; Vislobokova, 1990; Baygusheva and Titov, 2013). However, *P. pliotarandoides* does not display the comb-like bauplan of antlers that is a crucial diagnostic feature of *Eucladoceros*. The dichotomous bifurcation of crown tines appeared in the antler evolution of cervids independently several times, for instance, in *Rucervus schomburgki* and *Blastocerus dichotomus*.

Complete skulls have not been discovered for this species. However, based on the available evidence, the frontal bones are depressed in the front of the pedicles with a slightly concaved or straight sagittal profile. The angle of divergence between the pedicles is approximately 90°, and they are robust with circular transversal cross-sections, possibly slightly compressed anteroposteriorly. The basioccipital is bell-shaped and broadened in the area of pharyngeal tuberosities, and the foramen ovale is very large.

The upper dental row APL-243 from Apollonia (Croitor and Kostopoulos, 2004: fig. 4, B) and the upper dentition depicted by Flerov (1962) indicate that the lingual wall of P^2 is not cleft, and the interior wall of the premolar hypocone is slightly folded, which distinguishes this species from *Eucladoceros* and *P. obscurus*. Additionally, the upper molars lack the protoconal fold characteristic of *Eucladoceros*, and the spur of hypocone found in both *Eucladoceros* and *P. obscurus*. The advanced stage of P_4 molarization in the mandibles from Apollonia (APL-491, sin, Fig. A.36; APL-402, dex) further distinguishes this deer from *Eucladoceros*. The mandibles of *P. pliotarandoides* are characterized by a comparatively long lower premolar series, which makes up 70.7% and 72.8% of the length of the molar series. The mandibles are not pachyostosic.

Distribution. The remains of *P. pliotarandoides* have been frequently found in early Pleistocene faunas throughout Europe, but have often been reported under various names. Skull fragments with more or less complete antlers have been discovered in Psekups-Saratovskaja and Khaply, Russia (identified as *Eucladoceros* sp. and *E.* cf. *senezensis* by Alekseeva, 1977), Mariupol, Ukraine (identified as *E.* cf. *pliotarandoides* by Alekseeva, 1977), Aliakmon, Greece (identified as *Orthogonoceros verticornis* by Melentis, 1967), and Borgonuovo, Italy (identified as *Megaceroides verticornis* by Azzaroli, 1976). Additionally, a few remains from Salcia, Moldova and the Tamanian peninsula, Russia also belong to *P. pliotarandoides*. This species is a distinct element of pre-Galerian and Galerian faunas in the regions of South and South-East Europe. Notably, the occurrence of this species in the Ponto-Caspian area dates back much earlier. The chronological range of *P. pliotarandoides* is estimated to be approximately 2.2 Ma (Psekups-Saratovskaja) to 1.0 Ma (Apollonia) (Tesakov, 1995; Kostopoulos, 1997).

Praemegaceros (*Orthogonoceros*) *verticornis* (Dawkins, 1872)

Synonymy:

1872 *Cervus verticornis sp. nov.*: Dawkins, p. 406, fig. 2.
1883 *Cervus belgrandi* sp. nov.: Belgrand, pl. 7, figs. 1-2; pl. 8, fig. 1.
1899 *Cervus belgrandi* Lartet: Harmer, p. 106, pl. 21, fig. 1-4.
1920 *Cervus* (*Praedama*) *verticornis* (Dawkins, 1872): Portis, p. 132.
1927 *Cervus megaceros verticornis* (Dawkins, 1872): Soergel, p. 366.
1956 *Orthogonoceros verticornis* (Dawkins, 1872): Kahlke, p. 11.
1961 *Megaceros verticornis* (Dawkins, 1872): Azzaroli, p. 6.
1965 *Praemegaceros verticornis* (Dawkins, 1872): Kahlke, p. 381.
1967 *Megaceros* (*Megaceroides*) *verticornis* (Dawkins, 1872): Ambrosetti, p. 269.
1992 *Megaceroides verticornis* (Dawkins, 1872): Azzaroli and Mazza, p. 26-27.
1993 *Megaloceros verticornis* (Dawkins, 1872): Lister, p. 98.

Nomenclatural acts. The original description of *Cervus verticornis* included the description of two antlers of different sizes, believed to belong to mature and juvenile individuals (Dawkins, 1872: 407). Dawkins provided a detailed description of the larger "mature" specimen. Later, Newton (1882) designated the larger antler as the lectotype of the *C. verticornis* species. The original specimen is stored at the Norwich Museum. A cast of the lectotype, presented in 1867 by C. Falconer, is stored at the NHML (collection number M40835). The collection label does not specify the exact provenance locality, stating only that the specimen is "believed to be from the beach near Pakefield, Norfolk". Since the specimen selected by Newton (1882) preserves only the basal part of the antlers, Radulescu and Samson (1967) selected another better-preserved antlered skull from Pakefield (M11352, NHML) as a paratype of *P. verticornis*. Harmer (1899) described the specimen M11352 as *Cervus belgrandi* Lartet, which was considered a senior synonym of *Cervus verticornis*. Azzaroli (1953) and Radulesco and Samson (1967) suggested that "*C*." belgrandi from the Paris Basin is closely related to *P. dawkinsi* and may possibly be *synonymous* with it. The species name *Cervus belgrandi* first appeared in Belgrand's (1883) publication. The antler figured by Belgrand (1883: pl. 8, fig. 1) exhibits a vestigial dorsal tine, a characteristic feature shared with *P. dawkinsi*. Nevertheless, the deer from Paris Basin has a frontal breadth of 170 mm, making it significantly larger and approaching the size of giant deer, indicating that it is not identical with *P. dawkinsi*. It is possible that Belgrand's deer is closely related to *Praemegaceros mosbachensis*, however, unlike the latter species, the beam of Belgrand's deer is not flattened in the middle tine area.

Diagnosis. The body size is very large. Antlers are robust, with horizontal proximal portions and vertical distal portions oriented in the parasagittal plane. The antler base is perpendicular to the burr plane. The beam curves in the dorsal tine region and sharply turns upwards in the posterior tine region. A subbasal tine is generally absent. The dorsal tine is cylindrical, of moderate length, situated on the upper (medial) side of the beam and twisted towards the anterior. The middle tine is long, sharp, non-palmed, and is inserted on the anterior side of the beam. The distal portion above the posterior tine may be branched and somewhat compressed from the sides or may extend into a fan-shaped palmation. Pedicles are robust, diverged, dorso-ventrally compressed, and oriented in the frontal plane. The fourth premolar is typically molarized. The lingual walls of the upper premolars are not cleft or grooved. The hypocone of premolars is supplemented with a small interior enamel fold. Pachyostosis of the lower mandible is not developed. P_4 is molarized.

Lectotype. The type specimen M40835 (cast) is a basal fragment of the left shed antler that belongs to a large mature individual.

Locus typicus: Pakefield?, Norfolk, England.

Stratum typicum: the Middle Pleistocene of Cromer Forest-bed formation.

Description. The lectotype M40835 displays a circular and anteroposteriorly compressed antler base, lacking a developed subbasal tine. The dorsal tine arises from the upper (dorsal) side of the beam and measures 42 mm from its base to the antler burr. Over a preserved length of approximately 13 cm, the dorsal tine is cylindrical and curves anteriorly and downward. An accessory button-like prong is situated on the antler beam's lateral side adjacent to the dorsal tine. While not homologous to the subbasal tine, this accessory button constitutes a sort of hypermorphy. The middle tine emerges from the anterior side of the beam forward and represents a diagnostic characteristic distinguishing *P. verticornis* from *P. pliotarandoides*. The antler beam is moderately compressed dorsoventrally between the dorsal and middle tines, with a maximal diameter of 92.0 mm and a circumference of 275.0 mm at the base.

The stable development of the middle tine in *P. verticornis* is a crucial factor for distinguishing it from *P. pliotarandoides*. H.-D. Kahlke, in personal communication with Croitor and Kostopoulos (2004), notes that the middle tine is always present in *P. verticornis* from younger deposits of Mosbach and Süßenborn. Dawkins (1872, 1887) describes British specimens of *P. verticornis* with an always-present middle tine, which indicates that this feature is not variable. Pfeiffer (2002) describes a skeleton of a two-year-old antlered *P. verticornis* stag from Bilshausen (Germany) that possesses a strong, very long middle tine, along with dorsal, posterior, and crown tines. This finding confirms that the middle tine is present in *P. verticornis* at a very early stage of ontogenetic development. The pedicels of *P. verticornis* are sloped backward and sideward and strongly compressed in the dorsoventral direction.

The distal portion of the antler displays variations in shape among species of the genus *Praemegaceros*. The antlers recovered from the Süßenborn locality exhibit slightly compressed branched tines, analogous to the crown shape of *P. pliotarandoides* (Kahlke, 1956). Conversely, the antlered braincase from Pakefield in England displays a distinct distal part that extends into a broad fan-shaped palmation (Harmer, 1899). The presence of palmated and simple branched distal parts of antlers in *P. verticornis* may hold taxonomic significance at the subspecies or species level. Regrettably, this issue has yet to be resolved, given that the distal part of the type specimen of *P. verticornis* is absent.

The complete skulls of *P. verticornis* remain unknown, but the existing evidence indicates that the braincase is relatively short and broad. The basioccipital is bell-shaped and broad, while the frontal bones are flat, featuring dorso-ventrally compressed pedicles that slope sideward and backward, oriented in the forehead plane. The shape and position of these pedicles represent a taxonomic characteristic distinguishing *P. verticornis* from *P. pliotarandoides*. P_4 is generally molarized, while the lingual walls of the upper premolars do not display cleft or grooves. The hypocone of the premolars features a small interior enamel fold. The lower mandible's pachyostosis is not developed.

Subspecies. In 1967, Ambrosetti proposed distinguishing *P. verticornis dendroceros*, which possesses branched antlers, based on the well-preserved antlered frontlet Süß-3552 from Süßenborn, from the "typical *verticornis*" subspecies. The designation of the "typical *verticornis*" subspecies was accompanied by a figure of the specimen from Pakefield, even though the distal portion is missing in the lectotype of *P. verticornis*. Unfortunately, the attribution of the type antler to the subspecies indicated by Ambrosetti (1967) is impossible, as the specimen does not provide the necessary diagnostic characters. Thus, the nominotypical subspecies of *P. verticornis* cannot be determined. The situation is further complicated by the uncertainty regarding the species' type locality. Currently, the data on the antler variability of *P. verticornis* are incomplete, and it is not possible to define subspecies from the perspective of formal taxonomy.

Distribution. The Middle Pleistocene of England, Germany, Italy, Ukraine, and Moldova. Chronological span: 0.8 Ma (Tiraspol) – 0.4 Ma (Bilshausen) (Kahlke, 1971; Pfeiffer, 2002).

Genus *Candiacervus* Kuss, 1975

Nomenclatural acts. Simonelli (1907) classified the endemic deer from the Late Pleistocene of Crete within the genus *Anoglochis*, which is no longer in use as a valid taxonomical unit due to its artificial nature based on a single morphological characteristic, namely the high position of the antler ramification above the burr. Kuss (1975) subsequently proposed a new genus for the endemic cervids from Crete and other Mediterranean islands, namely *Candiacervus*. Kuss (1975) defined *Candiacervus* based on several morphological characteristics, including a small-to-medium body size, reduced or very small ethmoidal openings and preorbital pits, hypsodonty, the high position of the first time, and elongated and robust postcranial skeleton. Capasso Barbato

(1990) proposed that *Candiacervus* should be considered a subgenus of the genus *Megaceros*, which contained the informal "*verticornis*" group of large-sized continental deer (now the genus *Praemegaceros*). Kuss (1975) postulated that the Cretan deer represents an archaic lineage that evolved in isolation from a Middle Miocene forerunner and persisted until the Mindel Glaciation. Kuss (1975) also included cervid remains from Karpathos and Kassos in this genus. The genus comprises up to ten species that represent various stages of endemic evolution on Crete, Kasos, and Karpathos. It is possible that some species may be synonymous.

Diagnosis: deer of medium and small size with antlers that are secondarily simplified. The antler beam is sloped backward and sideward immediately from the burr. The basal tine is absent, while the other tines are reduced to varying degrees. However, the middle tine is typically present in all species. Cranial morphology is characterized by very small or reduced fissura nasolacrimalis and fossa praeorbitalis, a bell-shaped basioccipital, short nasal bones that do not reach the level of the anterior orbital edges, a complete absence of upper canines, and a moderately flexed and relatively short braincase. The pedicles are divergent and point sideways and backwards. The orbitofrontal is short, with the anterior edge of the orbits situated above M^2. Dentition is rather brachyodont, and the upper molars maintain hypoconal enamel spur. Additionally, the lower fourth premolar is molarized.

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

Candiacervus devosi van der Geer, 2018

Diagnosis. An insular cervid of intermediary body size. The fully grown antlers are four-pointed and maintain the dorsal (outer), middle, and posterior tines, which are homologous to the dorsal, middle, and posterior tines of the mainland *Praemegaceros*. The distance between the dorsal and middle tines is short. The antler beam is sharply turned upright and slightly sideways in the area of the posterior tine, while crown tines are absent. The dorsal part rim of the orbits is thick.

Holotype. The male skull AMPG(V)1735 figured in de Vos (1984: plate 13).

Paratype: right antler AMPG(V) 1733. Types are stored at the Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece (van der Geer, 2018).

Locus typicus: Liko Cave, Likotinara, Crete, Greece (van der Geer, 2018).

Stratum typicum: 75 uppermost centimetres of the Liko Cave filling.

Description. Van der Geer (2018) previously interpreted the two proximal antler tines as a double basal tine, but the present study suggests that the antlers of *C. devosi* maintain the antler bauplan characteristic of the mainland genus *Praemegaceros*. Similar to giant continental species, *C. devosi* is characterized by antlers that form a more or less sharp curvature in the area of the posterior tine. The homology of the dorsal and middle tines in *C. devosi* with the dorsal and middle tines in *P. verticornis* and *P. obcurus* is easily recognizable (Fig. A.34 E). However, unlike the continental species, *C. devosi* has lost crown antler tines. The proximal part of the antler does not exhibit the bending of the beam characteristic of *P. verticornis*. Instead, the sloped position of the beam to the burr suggests that the origin of *C. devosi* is related to *P. obscurus*.

While the frontal bones and pedicles of *C. devosi* maintain the same shape as those of the continental species, the skull morphology of this deer is already strongly influenced by the evolution in insular isolation. Specifically, the splanchnocranium is shortened, the orbits are shifted rostrally with respect to the upper tooth row, and the fossa praeorbitalis is vestigial.

Candiacervus listeri van der Geer, 2018

Diagnosis. The insular cervid of intermediary body size is characterized by fully grown antlers that are three-pointed, devoid of the dorsal tine and maintaining the middle and posterior tines. The height of the splanchnocranium is reduced due to the diminished volume of the nasal cavity, resulting in a concave face profile when viewed from the side, and elevated upper orbital margins above the frontal surface. The dorsal rim of orbits is thick.

Holotype: the male skull AMPG(V) 1734, figured in de Vos (1984, plate 12).

Paratype: the partial skull with left and right antler (AMPG(V) 1726) constitutes the paratype of the species. The type specimens are curated at the Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece (Van der Geer, 2018).

Locus typicus: Liko Cave, Likotinara, Crete, Greece (van der Geer, 2018).

Stratum typicum: 75 uppermost centimetres of the Liko Cave filling (van der Geer, 2018).

Description. The species under study represents a further stage in the evolution under insular isolation. Its antlers have lost both the proximal tines, namely the basal and dorsal tines, while retaining the middle and posterior tines. The antler beam exhibits the characteristic bending in the area of the posterior tine seen in continental *Praemegaceros*. Some specimens (van der Geer, 2018: fig. 8-3) preserve rudimentary crown tines. The antlers are moderately divergent and relatively long, measuring up to 60-70 cm (van der Geer, 2018). The proximal part of the antlers is compressed anteroposteriorly, a character that brings *C. listeri* closer to *Praemegaceros* from the Tiraspolian Gravel in Moldova. The antler surface is characterized by a moderate pearling, a specific feature that associates *Candiacervus* (and *Praemegaceros*) with the phylogenetic branch of *Cervus elaphus*. The facial portion of the skull is markedly low (van der Geer, 2018: fig. 8-1). This particular feature is likely linked to the reduction in nasal cavity volume and loss of olfactory abilities in the conditions of an unbalanced insular fauna that lacks terrestrial predators (Croitor et al., 2006).

Candiacervus rethymnensis Kuss, 1975

Diagnosis. The species exhibits an intermediate body size and features antlers with two tines in the proximal portion. The antler beam is moderately bent in its distal portion, resembling the mainland *Praemegaceros*. Some individuals may exhibit a supplementary proximal tine near the dorsal tine. The metapodials are elongated and maintain typical cervid proportions.

Holotype. The right metacarpal figured by Kuss (1975: pl. 6, fig. O), stored at the Natural History Museum, University of Crete, Heraklion, Greece.

Type locality. Mavro Muri 4, Crete (Kuss, 1975).

Description. Kuss (1975: pl. III, figs. C-E) described long antlers of this species, with only the middle tine preserved and a moderate bending that corresponds to the beam bending in the area of the posterior tine in the mainland *Praemegaceros*. These antlers are similar to those of van der Geer's *C. listeri*, suggesting the probable synonymy between the two species. Van der Geer (2018) identified the frontal fragment of the skull NHMH 38.70 with basal portions of antlers, likely from Melidoni, as belonging to *C. rethymnensis*. This specimen is characterized by the presence of a supplementary proximal tine situated close to the dorsal tine on its left antler, which has a more medial position, and the middle tine with a more lateral position. This additional tine likely represents an individual variation and has no taxonomic value. The specimen from Melidoni should instead be assigned to *Candiacervus devosi*.

Candiacervus ropalophorus de Vos, 1984

Diagnosis. The species is characterized by a small body size with a shoulder height of about 40 cm. The antlers are remarkably long, disproportionally to the body size, reaching up to 77 cm, and may exceed the total head-to-tail length. Antlers are characterized by a small tine located at a certain distance from the burr and the development of a distinctive bludgeon-like formation in their distal part. Limb bones are short and robust.

Holotype: the male skull Ge4-46, figured in de Vos (1984: pl. 10).

Paratype: antler RGM 438460. Types are stored at the Naturalis Biodiversity Center, Leiden, the Netherlands (van der Geer, 2018).

Locus typicus: Gerani IV, Crete (van der Geer, 2018).

Stratum typicum: 40 uppermost centimetres of the Gerani Cave filling (van der Geer, 2018).

Distribution: Known from the Mindel Glaciation (?) to historical times on the island of Crete (Kuss, 1975).

Description. The species is characterized by a relatively thin and delicate skull shape and proportions (Schilling and Roessner, 2021: fig. 1). The face profile between the orbits is concave, but the upper margins of the orbits are not elevated above the frontal plane. The splanchnocranium is relatively short and thin, and the facial portion of the skull before the orbits is very low. The muzzle is narrow, and the praemaxillary bones are rectangular-shaped and broad. The nasopremaxillary suture is moderately short. The orbitofrontal part of the skull is short, with the anterior edges of the orbits situated above the posterior part of M^2. The nasal bones are short and do not reach the level of the anterior orbital edges. In contrast to *C. cretensis*, the orbits are less oblique in the dorsal view, indicating that *C. ropalophorus* did not have partial binocular vision. The braincase length measured from bregma to inion equals the maximum braincase breadth in females and behind pedicles in males (Schilling and Rössner, 2021) and may be classified as relatively short. The basicranium is moderately broadened at pharyngeal tuberosities, giving it a bell-shaped appearance. Upper canines are completely lost, and the frontal bones are flat between pedicles. The pedicles are sloped backward and sideward.

Candiacervus cretensis (Simonelli, 1907)

Diagnosis. The species is characterized by its small body size, reaching approximately 55 cm at the shoulder. The splanchnocranium is low and the face profile is concave in the side view. The upper margins of the orbits are elevated above the frontal surface, and the dorsal rim of the orbits is thick. The muzzle is relatively narrow, and the premaxillary bones are rectangular in shape. Antlers are typically two-pointed and relatively small, with a thin main beam that has a subtriangular cross-section in its proximal part and is flattened in the distal portion. The tine on the anterior side of the beam is situated at a distance of about one-third of the total antler length from the burr. Metapodials are short and robust.

Type locality. Mavro Muri 4, Crete.

Holotype. Not yet established. A lectotype should be determined from Simonelli's material (Kuss, 1975).

Locus typicus: karst formation near Grida Avláki (see Kuss, 1970).

Stratum typicum: Grida-Avláki level, probably Riss/ Würm interglacial (Kuss, 1975).

Distribution: Known from the Mindel Glaciation (?) to historical times on the island of Crete (Kuss, 1975).

Description. *Candiacervus cretensis* represents a stage of evolutionary adaptation to insular isolation, characterized by a reduction in body size and further simplification of antlers. It is very similar to *C. rethymnensis*, but 30-50% smaller according to Kuss (1975), and shares a cranial morphology with *C. listeri*. The orbits are obliquely oriented on the skull, allowing for partial binocular vision (Simonelli, 1907; Kuss, 1975). Antlers consist of a main beam with a flattened distal portion that preserves the middle tine, and are generally thinner than the pedicle. Individual variations in antlers are broad, with some specimens evolving additional tines that may be considered atavistic. For instance, Kuss (1975: pl. 3, fig. A) describes an interesting antler variant that evolved a small distal palmation, a posterior tine, and a small basal tine close to the burr, similar to *Praemegaceros obscurus*. Other antler variants with bifurcated tines (Kuss, 1975: pl. 3, fig. A) may be considered hypertrophic or hypermorphic.

Candiacervus reumeri van der Geer, 2018

Diagnosis: The insular cervid of intermediary body size. The fully grown antlers are four-pointed. The antler beam is sloped backwards immediately from the burr. Antlers are characterized by the presence of two well-developed tines inserted on the anterior side of the beam and the distal fork. The distances between the burr, tines and distal fork are roughly similar. The dorsal wall of the orbital wall is very thin. The upper orbital margins are not elevated above the frontal surface.

Holotype: the male skull AMPG(V) 1736, figured in de Vos (1984, pl. 14).

Paratype: the left antler RGM 442702 (figured in de Vos (1984, pl. 8). Type specimens are stored at the Museum of Palaeontology and Geology, National and Kapodistrian University of Athens (Greece) (holotype) and the Naturalis Biodiversity Center, Leiden, the Netherlands (paratype) (van der Geer, 2018).

Locus typicus: Liko Cave, Likotinara, Crete, Greece (van der Geer, 2018).

Stratum typicum: 75 uppermost centimetres of the Liko Cave filling (van der Geer, 2018).

Description. *Candiacervus reumeri* is a species of deer that exhibits a different antler bauplan compared to the previously described species, *C. ropalophorus* and *C. cretensis*. However, *C. reumeri* shares certain morphological features with *C. devosi* and *C. listeri* that suggest a common evolutionary origin. These shared features include the oblique position of the beam axis to the burr and the concave anterior side of the proximal part of the antler. One can assume that the antler bauplan of the *devosi-listeri* lineage and the *reumeri* lineage represent two distinct evolutionary modifications of the same initial bauplan. In the case of the *devosi-listeri* lineage that evolved on Crete, the proximal portion of the antler beam became progressively shortened, resulting in a very short distance between the dorsal and middle tines. However, in the case of the *reumeri* lineage, the progressive shortening affected the distal portion of the antlers, which transformed into a distal fork. In some specimens, this distal fork is composed of a stronger anterior tine that represents the continuation of the beam, and the posterior tine that is a homology of the posterior tine in *C. devosi*, *Praemegaceros verticornis*, and *P. obscurus*.

Candiacervus pigadiensis (Kuss, 1975)

Diagnosis: an intermediate-sized deer species with unspecialized limb proportions. The fully grown antlers of this species have four tines of approximately the same size, all located on the anterior side of the beam. The most proximal tine is positioned at a certain distance from the burr. The distance between the tines is relatively equal, resulting in a comb-like pattern. The antler cross-section is irregularly circular in shape.

Holotype: The right tibia, 205 mm long (Kuss, 1975: pl. IV, fig. 1). Collection of the Geological and Paleontological Institute of the University of Freiburg.

Locus typicus: Kandilia cave, the Island of Karpathos, Greece, 1.5 km southeast of Pigadia (Kuss, 1975).

Stratum typicum: Probably Riss / Würm interglacial (Kuss, 1975).

Distribution: islands of Karpathos and Kasos.

Description. This is a species of deer with antlers that sometimes develop a multiaxial crown composed of 3-4 short tines. The right tibia of this species is 205 mm long and exceeds the length of the tibia of *C. cerigensis* by approximately 20% (Kuss, 1975: tab. IV, fig. 1). The antlers of *C. pigadiensis* have a comb-like shape, which is an interesting morphological feature that superficially resembles continental *Eucladoceros*. However, unlike *Eucladoceros*, the distal portion of antlers in *C. pigadiensis* is not flattened. Some antler variants from Karpathos that are attributed to *C. pigadiensis* by Kuss (1975) form a multiaxial small crown composed of three or four short tines. This morphological feature is reminiscent of *Cervus elaphus* of the modern type and may suggest a more complicated pattern of colonization of Karpathos by continental cervids. The body size, limb proportions, and antler shape of *C. pigadiensis* are very similar to those of *C. reumeri*, leading to speculation that the two species may be synonymous. The close morphological affinity between *C. pigadiensis* and *C. reumeri* also suggests that the main evolutionary processes of the *pigadiensis-reumeri* lineage took place on Karpathos and Kasos. The presence of *C. reumeri* on Crete indicates that the *pigadiensis-reumeri* lineage dispersed into Crete via the landbridge that emerged during one of the phases of the sea level lowering.

Candiacervus cerigensis (Kuss, 1975)

Emended diagnosis. A small-sized deer species with short and robust limbs. Its antlers are five-pointed and arranged in a comb-like pattern, with the distal portions of the antlers not flattened. The muzzle is relatively short compared to that of *C. cretensis*.

Holotype: left antler rod with 5 ends (panel III, figure f).

Locus typicus: Kandilia Cave, 1.5 km southeast of Pigadia, Karpathos Island.

Stratum typicum: Probably Riss / Würm interglacial (Kuss, 1975).

Description. Based on the morphology of *C. cerigensis* antlers (Kuss, 1975: tab. III, fig. F; tab. IV, fig. C, E, I, M, Q), it appears that this species is closely related to *C. reumeri*. *C. cerigensis* is a highly specialized insular endemic, as evidenced by the advanced shortening of the splanchoocranium, small body size, and short, robust limbs. Despite its insular adaptations, *C. cerigensis* has maintained a relatively complex antler morphology with up to five tines.

Genus *Cervus* Linnaeus 1758

Synonymy:

Pseudodama Azzaroli, 1992

Euraxis Di Stefano and Petronio, 1998

Diagnosis: these deer vary in size from small to large and have a pearled antler surface. Antlers always have the basal (brow) and middle (trez) tines, and the crown is represented by a distal fork in the simplest variants. Cross-sections of antler beam and proximal and trez tines are circular. The braincase is rather short, with the breadth exceeding the distance between bregma and inion. The basioccipital is narrow and wedge-shaped, not extending at the level of pharyngeal tuberosities. Pedicles are moderately long, moderately divergent, and deflected caudally. Small upper canines are always present, and nasal bones are short, never reaching the level of anterior edges of orbits. In most species, the splanchnocranium is relatively long.

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).

Cervus nestii (Azzaroli, 1947)

Synonymy:

1879 *Cervus Nestii nomen nudum*: Forsyth Major, p. C.

1947 *Dama nestii nestii* (F. Major): Azzaroli, p. 54, fig. 4 (4).

1992 *Pseudodama lyra* sp.nov.: Azzaroli, p. 6, Fig. 2, pl. 1, fig. 1 a-c.

1992 *Pseudodama nestii* (Azzaroli): Azzaroli, p. 12, figs 5-7.

1995 *Cervus* (*Dama*) *cf. nestii* (Major): Vekua, p. 124, tab. 44, fig. 3.

1997 *Dama* (*Pseudodama*) *nestii* (Azzaroli): Pfeiffer, p. 34.

1998 *Euraxis lyra* (Azzaroli): Di Stefano & Petronio, p. 52.

1998 *Euraxis nestii* (Azzaroli): Di Stefano & Petronio, p. 52.

2001 *Cervus abesalomi sp. nov.*: Kahlke, p. 475.

2003 *Axis nestii* (Azzaroli): Girotti *et al*., p. 88, fig. 3a-d.

Nomenclatural acts: Forsyth Major's (1879, *n.v.*) original citation of the species name *Cervus Nestii* was not accompanied by a species description, a type designation and a describing figure (*fide* Azzaroli, 1992). Azzaroli (1947) proposed the description of the subspecies *Dama nestii nestii* F. Major and figured the type specimen. Later, Azzaroli (1992) considered Forsyth Major's *Cervus Nestii* as *nomen nudum* and suggested that the authorship of the species "*nestii*" belongs to Azzaroli 1947. The formal diagnosis of the species was not proposed. The species name "*nestii*" is used here *sensu* Azzaroli (1992). Later, Azzaroli (1992) created a new genus *Pseudodama* with the type species *Dama nestii nestii* Azzaroli, 1947 and several other Late Pliocene and Early Pleistocene "*Dama*-like" deer: *Cervus pardinensis* Croizet and Jobert, 1828; *Cervus rhenanus* Dubois, 1905; *Cervus perolensis* Azzaroli, 1952; *Pseudodama lyra* Azzaroli, 1992; and *Pseudodama farnetensis* Azzaroli, 1992. The enlisted species share a similar body size comparable to that of modern fallow deer (hence the term "*Dama*-like deer") and simple lyre-shaped antlers with three or four tines. However, the genus *Pseudodama* caused controversial opinions, as many authors agreed that *Pseudodama* is a polyphyletic taxon (de Vos et al. 1995; Croitor 2001, 2006b, 2012; di Stefano and Petronio 2002). Di Stefano and Petronio (1998) created the genus *Euraxis* with *Dama nestii* Azzaroli, 1947 as a type species that implies the synonymy between *Pseudodama* and *Euraxis*. Later, Di Stefano and Petronio (2002) included the "*Dama*-like" species in the modern genera *Axis* (including *Cervus nestii*) and *Rusa*. Pfeiffer (1999) regarded Azzaroli's *Pseudodama* as a subgenus of the genus *Dama*.

Diagnosis: A medium-sized deer with body size similar to modern fallow deer. The braincase is unflexed with flattened parietal bones. The facial portion of the skull is relatively long: the orbitofrontal region of the skull is elongated as in *Cervus*. The anterior edge of the orbit does not reach the level of M^3. The posterior edge of nasal bones does not reach the line connecting the anterior edges of orbits. The distance between P^2 and prosthion is shorter than the upper tooth row. Pedicels are long and sloped from the face toward the posterior. Frontal bones are flat. The lower mandible has a more open angle (110°) between horizontal and ascending parts if compared to fallow deer. The angle between the labial and lingual sides of the upper molars is comparatively narrow and amounts to 30°. The morphology of P_4 is primitive. Antlers are four-pointed and thin, with a pearled surface. The first (brow) tine is situated at a certain distance from the burr. The middle (trez) tine is well-developed. The distal bifurcation is oriented in the frontal plane. Metapodial bones are short. The metacarpus is shorter than the radius.

Holotype: a pair of antlers with pedicels and frontal bones IGF 363, MGUF. The major part of the left antler is restored.

Type locality: Tasso, Upper Valdarno, Central Italy.

Stratum typicum: late Villafranchian deposits of Upper Valdarno.

Description. The estimated body size of *Cervus nestii* is approximately 70 kg. The type specimen IGF 363 (MGUF) from Upper Valdarno is a pair of antlers belonging to a mature individual. The antlers are thin, long, and four-pointed, the antler surface is pearled. The first tine is situated at a certain distance from the burr, and the bez tine (an additional basal tine often present in red deer) is always missing. The middle (trez) tine is well-developed. The first segment of the beam (the portion between the first and middle tines) is somewhat longer than the second segment (the beam portion between the middle tine and the distal bifurcation). The distal bifurcation is formed by two short tines of almost equal size and is oriented in the frontal plane. The pedicels are moderately long (L, 19.8 mm; DAP×DLM, 27.5×30.5 mm [sin]; L, 22.5 mm; DAP×DLM, 27.1×29.5 mm [dx]) and somewhat inclined caudally. The frontal orientation of the distal fork reminds of the primitive fossil and modern subspecies *C. elaphus acoronatus* and *C. elaphus bactrianus*. The antlers of *C. nestii* are very similar to those of the subspecies *C. elaphus barbarus* Bennett from North Africa that lack the bez tine too.

The fairly complete but damaged antlered skull of a young adult male IGF 243 (MGUF) of *Cervus nestii* from Figline (Fig. A.37) is characterized by an unflexed braincase with flattened parietal bones. The face is very long, with the ratio of face length (measured from the anterior edge of orbit to prosthion) / condylobasal length amounting to 61.2%. The variation range of the face length / condylobasal length index is 58.6 - 61.0% in *C. elaphus elaphus* (n=5), 52.8 - 55.1% in *C. nippon* (n=3), and 52.3 - 56.5% in *Dama dama* (n=13). The projection of the anterior edge of the orbit runs down behind M^3. The posterior edge of the nasal bones does not reach the line connecting the anterior edges of the orbits. The nasal bones have very short contact with ethmoidal openings (shorter than ½ of the ethmoidal opening length). The preorbital fossae are deep. Pedicels are long and sloped from the face caudally. Frontal bones are flat and just slightly depressed between orbits. The horizontal ramus of the mandible forms an open angle (110°) with the ascending mandibular part. The upper canines are present. The angle between the labial and lingual walls of upper molars is comparatively narrow, amounting to 30°. The morphology of P_4 is primitive. The lower premolar series attains 64.3% of the molar series length in specimen IGF 243, falling within the range of variation of modern European red deer (60.3% - 65.2% according to the sample stored in NMNH). The cranial morphology suggests that *C. nestii* is one of the earliest representatives of the *elaphus* group, showing a greater affinity with *C. elaphus* than with *C. nippon*.

Distribution. Early Pleistocene of Italy and Georgia. Additionally to the type locality, it has been reported in Olivola, Italy (Croitor, 2014), and in Dmanisi, Georgia, where it was previously described as *C. abesalomi* Kahlke, 2001 (Croitor, 2006b; Bukhsianidze, 2016).

Cervus elaphus Linnaeus, 1758

C. elaphus acoronatus Beninde, 1937 is the most archaic subspecies of red deer that dispersed in Europe by the beginning of the Middle Pleistocene. This is a large-sized form characterized by the advanced molarization of P_4 and the presence of the bez tine as in modern *C. elaphus*. The distal part of antlers ends in a simple transversal distal fork as in *C. nestii* and the modern subspecies *C. elaphus bactrianus* Lydekker, 1900 and *C. elaphus yarkandensis* Blanford, 1892. *Cervus reichenaui* Kahlke, 1996 (= *Cervus elaphoides* Kahlke, 1960) from the early Middle Pleistocene of Mosbach is based on antler remains of a young individual of red deer and has been identified by Lister (1990) as a junior synonym of *C. e. acoronatus*. The lower mandible proportions of specimen 32863/17 (SMNH) from Mosbach fall within the range of variation observed in modern red deer, with the relative length of diastema to lower tooth length being 74.9%, and the premolar to molar series length ratio being 61.3%. The Mosbach specimen's measurements correspond to the comparatively moderate body mass of 170 kg observed in red deer.

C. elaphus angulatus Beninde, 1937, from the Late Middle Pleistocene of Steinheim (250 kyr: Geist, 1998), is a direct descendant of *C. e. acoronatus* that evolved the most unusual shape of its distal crown. Young individuals of this subspecies evolve antlers similar to those of *acoronatus*, with a simple frontally oriented distal fork, as observed in the specimen ST-18176 (SMNH). The fully grown antlers' distal part may vary, but there is a general and specific morphological pattern: the beam segment above the middle tine is more robust than the beam segment below the middle tine. The antler crown preserves the initial distal fork, but it develops a very strong and long caudal tine, which forms a right antler with the beam and is directed posteromedially. This caudal crown tine often extends into a small horizontal palmation that bears additional tines (up to six). The functional significance of the caudal crown tine is not clear, but it possibly had the same function as the posterior tine in *M. giganteus* and *R. tarandus* and other deer adapted to the open or/and wet landscapes: the function of removing the flying parasites from the back in rutting males, thus increasing their combat capacities (Croitor, 2016). According to Geist

(1998), the red deer of the angulatus-type survived in the Iberian glacial refugium, and a high percentage of the south Spanish deer carry this diagnostic antler form.

Italy has yielded several endemic red deer forms due to its higher biogeographic isolation and connection with the Balkan Peninsula. *C. elaphus rianensis* Leonardi and Petronio, 1974, from the Aurelian Age of the Middle Pleistocene of Italy, is a distinct descendant of *C. e. acoronatus*, characterized by antlers terminated with a distal fork. This contemporaneous with *C. e. angulatus* form of red deer is distinguished by its smaller body size (male body mass is approximately 130 kg), relatively short limbs, and shortened distal beam segment between the trez tine and the distal fork (Leonardi and Petronio, 1974). The slightly older *C. elaphus eostephanoceros* Di Stefano and Petronio, 1993, from the late Galerian Age of Cava Nera Molinario (Italy), is a junior synonym of *C. e. rianensis*. The type antler of *C. e. eostephanoceros* is characterized by a shortened distal part above the trez tine, as in *C. e. rianensis* (Di Stefano and Petronio, 1993: fig. 2).

C. elaphus siciliae Pohlig, 1893, from the end of the Middle-Late Pleistocene of Sicily, is a slightly smaller deer (approximately 100 – 110 kg) with specific adaptations to grazing: the facial tubercle zone is particularly rough, the stout and the mandibular diastema are relatively short, the premaxillary bones are broad and squared, and the mandibular body is relatively high (Gliozzi et al. 1993). The advanced morphological character is seen in more divergent and short pedicles compared to modern red deer. Antlers are simplified: in 40% of specimens, the bez tine is missing; the trez tine may also be vestigial or completely absent; the distal part of the antler is formed by two or three tines (Gliozzi et al., 1993).

C. elaphus aretinus Azzaroli, 1961, from the last interglacial phase of Val di Chiana (Italy), represents a different dispersal event of red deer. This subspecies is characterized by the absence of bez tine, the long trez tine, and a massive distal crown, which, however, is simple and resembles the *C. elaphus maral* type: the crown is formed by a stronger posterior axial tine and multiple "secondary" tines (up to five) that are inserted on the main crown axis (Azzaroli, 1961; Croitor and Cojocaru, 2016). Another antlered skull with maral-like antlers is reported from the Late Pleistocene of Liguria (Le Prince, Italy) (Barral and Simone, 1968: 87, fig. 14-1). *C. elaphus aretinus* is closely related to, or may even be synonymous with, Caucasian and Caspian red deer *Cervus elaphus maral* Lydekker, 1898. The Balkan-Anatolian-Caucasian glacial refugium is the area of origin and the center of dispersal of *C. elaphus maral* (Sommer et al. 2008; Meiri et al. 2013). Perhaps, *C. elaphus aretinus* entered the Italian Peninsula via the narrow passageway between the Alps and the Dinaric Alps.

The remains of *Cervus elaphus barbarus* Bennett, 1833 from the Late Pleistocene era in Doukkala II (Morocco) are characterized by advanced molarization of P_4, a missing bez antler tine, and moderate body size, similar to the coeval Würmian red deer from Comb Grenal in southwestern France (Laquay, 1986). According to Laquay's (1986) dental measurements, the estimated body mass of a male individual from Doukkala-II is approximately 220 kg. Adult individuals of the modern Barbary stag *C. e. barbarus* exhibit a primitive type of pelage color with white spots on their back in adulthood, which Geist (1998) regards as a paedomorphic feature. The exact time of red deer dispersal in Africa is unknown. The presence of red deer in northwestern Africa is known only from the Late Pleistocene period. Gentry (2010) reported a single cervid molar of older Pleistocene age from the Nile Valley in Sudan. Finally, Ludt et al. (2003) found a surprisingly high genetic differentiation of modern *C. e. barbarus* from other subgroups of modern red deer, with a time of divergence of around 2.2 million years ago, which roughly coincides with the dispersal of *Cervus nestii* in the Ponto-Mediterranean area.

Cervus canadensis Erxleben, 1777

Synonymy

1777 *Cervus canadensis* [sp. nov.]: Erxleben, p. 305.
1836 *Cervus canadensis* Brisson: Schroeber, p. 990, tab. 246A.
1836 *Cervus strongyloceros* [sp. nov.]: Schroeber, p. 1074, tabs. 247F-G.
1846 *Cervus* (*Strongyloceros*) *spelaeus* [sp. nov.]: Owen, p. 469, fig. 193.
1873 *Cervus maral sibirica* [sp. nov.]: Severtzoff, p. 109, fig. p. 105.
1898 *Cervus canadensis asiaticus* Severtzoff: Lydekker, p. 104, fig. 27, Pl. 6.
1915 *Cervus canadensis baicalensis* nom. nov.: Lydekker, p. 134.
1947 *Cervus elaphus sibiricus* Severtzov: Heptner and Tzalkin, p. 77.
1952 *Cervus elaphus canadensis* Erxleben: Flerov, p. 175, fig. 55.
1952 *Strongyloceros spelaeus* Owen: Friant, p. 1398.
1959 *Cervus elaphus sibiricus* Severtzov: Sokolov, p. 217, fig. 44.
1987 *Cervus elaphus* Linnaeus: Lister, p. 193.
2005 *Cervus elaphus cherskii* ssp. nov.: Boeskorov, p. 76, fig. 2.

Nomenclatural acts. Schroeber (1836) granted the authorship of the species *Cervus canadensis* to Brisson (1756). Nonetheless, Brisson's "Regnum Animale" is regarded today as unavailable for zoological taxonomy work, since Brisson (1756) did not apply the binominal zoological nomenclature in his species descriptions. Although several important generic names are currently accepted as from Brisson (Gentry, 1994), none of his specific names is accepted as available. Regarding the case of *Cervus canadensis* in particular, we want to indicate that "Cervus Canadensis" mentioned in Brisson (1756) is quoted from Ray (1693: p. 84) where it was used together with "Cervus Europaeus" as an indication to the geographic provenance of the common deer *Cervus*, not a binominal term. Therefore, these quotations should not be regarded as available species designations.

Thus, Erxleben (1777) was the first who introduced the binominal species name *Cervus canadensis* for the Canadian stag. Schroeber (1836) himself proposed a new species name for a large North American deer *Cervus strongyloceros* accompanied by a brief description and figures representing the pelage colour of a female and a shed antler. In the same work, Schroeber (1836) published a description of *Cervus canadensis* Brisson supplemented with a figure of a stag with fantastic undulated antlers, suggesting that the author was poorly acquainted with this species. Severtzoff (1873, 1876) was the first who noticed the striking resemblance between Siberian "*Cervus maral*" (should not be confused with the name *Cervus elaphus maral* Ogilby given to Caspian red deer) and North American *Cervus canadensis*, indicating that the only difference between those two cervid forms is that Canadian deer have no the seasonal change the pelage colour (this observation was made only on two captive individuals).

Lydekker (1898) regarded wapiti as the true species *Cervus canadensis* and introduced for Asian wapiti a new subspecies name *C. canadensis asiaticus*, which represents a modification of *Cervus maral asiatica* quoted from Severtzoff (1873). According to Allen (1930), Severtzoff (1873) used the term *asiatica* in a group sense, not as a technical name, and therefore it should be rejected, while the name *C. canadensis asiaticus* should have to date from Lydekker (1898).

Heptner and Zalkin (1947: p. 69) consider that populations of Siberian wapiti in natural conditions are genetically isolated from Western and Central Asian red deer, stressing, however, that the areas of distribution of Asian wapitis and red deer forms never overlap, therefore most probably we are dealing with subspecies of the same species. The easy hybridization between wapiti and red deer also is regarded by Heptner and Zalkin (1947) as an argument for including various geographical elaphine forms as subspecies in the single species *Cervus elaphus*.

Flerov (1952: p. 175) included Asian wapitis in the subspecies *C. elaphus canadensis* together with North American wapitis. Sokolov (1959) rejected Flerov's (1952) viewpoint and suggested that the remarkable similarity in pelage colouring and antler shape of *Cervus elaphus sibiricus* Severtzov and *Cervus elaphus canadensis* Erxleben should be regarded as an evolutionary parallelism and prefers to keep those two elaphine forms as distinct subspecies of *Cervus elaphus* Linnaeus. Schonewald (1994) arrived to the conclusion that the differences in behaviour (male vocalization), sexual dimorphism differences, and semi-lethal hybridization support the species rank of *Cervus canadensis*.

Description. The specimen Nr. 381 (IZC) from the Late Pleistocene of Climăuți II (Moldova) represents a distal portion of the left antler with the basal part of middle (trez) tine and partially preserved crown tines (Fig. A.38). The antler surface is sculptured with weak longitudinal ribs and furrows and is covered with fine pearling, which is quite weak if compared to *Cervus elaphus*. The middle tine springs off sideward and forms with the beam an angle of 80^0. The crown shape represents a typical *Cervus canadensis* comb-like morphological pattern. The antler crown consists of three tines that are situated almost in the same plane (more or less parasagittal to the animal's body axe). The first crown tine is the strongest one and is the longest tine as it is typical for *Cervus canadensis*. The two distal tines of the antler crown are somewhat curved inward (toward the sagittal plane). The antler beam is cylindrical between the middle tine and the distal crown; however, the antler becomes somewhat flattened in the area of bifurcations. The shape of the middle tine is circular, while the crown tines are significantly compressed from the sides.

The circumference of the antler beam between the bez and trez tines of the specimen Nr. 381 is just slightly below the mean value of antler circumference above bez tine of the sample of modern *C. canadensis* from North America reported by Lydekker (1898) and is slightly larger than the maximal value of the sample of antlers of modern *Cervus canadensis* from Alaska reported by Boeskorov (2005). We do not exclude that the sample described by Lydekker (1898) includes exceptionally large hunter trophies. The antler of wapiti from Climăuți II corresponds to the most robust antlers of *C. canadensis cherskii* from the Late Pleistocene of Eastern Siberia. The length of the beam segment between the trez tine and the first crown tine is absolutely and relatively significantly longer in the antler from Climăuți II than in the holotype of *C. canadensis cherskii* (ca. 147 mm; measured from Fig. 2d in Boeskorov, 2005) to the circumference of beam segment between bez and trez tines, which attains 190 mm in the holotype of *C. canadensis cherskii*.

The second specimen Nr. 382 represents a portion of the beam (ca. 37 cm length) in the area of trez tine bifurcation that belongs to a somewhat larger antler: DLM and DAP of the beam above the middle tine bifurcation amount correspondingly to 64.3 mm and 64.5 mm. The beam circumference above the middle tine places this specimen among the most robust wapiti antlers.

The occurrence of wapiti in South-Eastern Europe was recently attested by the analysis of mitochondrial DNA sequences from Late Pleistocene remains of elaphine deer from the Emine-Bair-Khosar Cave in Crimea, Ukraine (Stankovic et al. 2011). The absolute age of the specimens in question is 33,100 ± 400 BP and 42,000 ± 1200 BP (*ibidem*). The mitochondrial DNA extracted from large elaphine deer remains discovered in the Peştera cu Oase site (MIS 3, Romania) indicate clearly that the Romanian sample falls within the “wapitoid” clade (Parfitt and Lister, 2013).

The presence of *C. canadensis* in the Late Pleistocene of Europe is confirmed by the finding of the antler fragments from the upper layer of the Paleolithic site of Climăuți II dated to 20 350 ± 230 y. BP. The antler fragments from Climăuți II are exceptionally large in comparison to those of modern red deer and, what is most important, one of the specimens is a distal part of an antler that represents a comb-like morphological pattern of crown shape typical for *Cervus canadensis*. The antler crown consists of three tines that are situated almost in the same plane (more or less parasagittal to the animal's main body axis). Perhaps, the remains of *C. canadensis* are more frequent in the Late Pleistocene of Europe, but they in most cases are misunderstood since the details of the craniodental morphology of this species are little known. The following subspecies of wapiti may be regarded as valid.

Subspecies:

Cervus canadensis spelaeus Owen, 1846

The extremely large basal antler portion from the Late Pleistocene deposits of Kent's Cavern (England) described by Owen (1846) as *Cervus* (*Strongyloceros*) *spelaeus* provoked the long-lasting debate on the presence of wapiti (*Cervus canadensis*) in the Late Pleistocene of Europe. The specimen from Kent's Cavern recalls European red deer morphology but with large dimensions approaching the largest modern North American wapiti antlers. *Cervus strongyloceros* Schreber, 1836 (one of the synonyms of *C. canadensis* Erxleben) is the type species of *Strongyloceros* Owen, 1846. Lydekker (1915) regarded *Strongyloceros* as a junior synonym of *Cervus* and this viewpoint was generally followed since then. By the end of the XIX century, several reports on the presence of large fossil wapiti-like deer in Europe appeared in the scientific literature (see Belgrand, 1883: pl. 22, fig. 1). The analysis of mitochondrial DNA of some elaphine deer remains from Kent's Cavern revealed that they belong to European red deer *Cervus elaphus* (Meiri et al., 2013), therefore the question on the presence of wapiti in the fauna from Kent's Cavern remains open. According to Geist (1998), the cave stag from Kent's Cave was most likely a wapiti. The antler of *C. canadensis spelaeus* bears two basal tines (brow and bez) separated by a certain distance; the circumference of the beam between the brow and the bez tines, according to Owen (1846), measures 381 mm (15 inches) and significantly exceeds the maximal value for modern American wapiti (330.2 mm) reported by Ward (1892). This value exceeds by ca. 30% the circumferences of other fossil forms of wapiti. The circumference above the burr attains 375 mm, thus greatly exceeding the analogous measurements of modern European red deer *Cervus elaphus* Linnaeus, which range between 220 and 230 mm (Friant, 1957). According to Geist (1998), the basal beam circumference indicates a predicted condylobasal length of 528 mm and a body weight of at least 550 kg lean. The circumferences above the burr of other antlers found in Kent's Cavern range from 25 to 30 cm (Lister, 1987a) and correspond to the values of the largest modern American wapitis (Geist, 1998). Besides the exceptionally large size, not much could be said about the cave stag. The distal fragments of wapiti antlers described from the Late Paleolithic site Climauți II are characterized by exceptionally large size and possibly represent a wapiti similar to the cave stag. The length of the segment between the trez tine and the first crown tine amounts to 410 mm and exceeds by ca. 38% the analogous measurement of other known fossil forms of wapiti (Croitor and Obada, 2018). Most of Kent's Cavern fauna from the main cave deposits has a pre-LMG age and is dated back to 50000–25000 years before the present (Higham et al., 2011).

Possibly, the mandible 2003-4-420-Sol of a large-sized deer from the Pleistocene of Soleilhac (France) that was originally described as *Megaceros* (*Megaceroides*) *solilhacus* by Azzaroli (1979, pl. 3, fig. 2) also belongs to *C. canadensis*. Besides the extremely large size (Tab. A.7), this specimen from Soleilhac is characterized by a very long diastema. The length ratio between diastema and lower cheek tooth row is 82.6%, approaching the mandible 2003-4-420-Sol to modern red deer and distinguishing it from other Pleistocene large-sized deer (Croitor et al., 2006). The mandible in question comes from the old paleontological collections of Musée Crozatier (Le Puy-el-Velay, Haute-Loire, France), so its exact stratigraphic origin is unknown.

Cervus canadensis palmidactyloceros De Stefano, 1911

Numerous remains of a peculiar deer come from the Late Pleistocene and Early Holocene of Northern Italy and the peat bogs of Switzerland (Rütimeyer, 1861; De Stefano, 1911). The rather heavy antler beams are directed sideward and terminated with a strongly flattened crown segment that bears four tines (Figs. 9C, 10B). This strong divergence of antlers may be seen also in the antlered skull from Settecannelle, Italy (Abbazzi, 1995b: figs. 5, 7). De Stefano (1911) reported the remarkably large size of the skeletal remains of this deer and the development of a distal palmation that varies in breadth from 142 to 190 mm. All palmations figured by De Stefano (1911) and Abbazzi (1995b) generally show a constant shape pattern: three crown tines that terminate palmation are situated in the same parasagittal plane; the first crown tine is the strongest one and in all cases is bifurcated. Sometimes this bifurcation is set in the transversal plane or looks like a small accessory prong of the stronger first crown tine (De Stefano, 1911). The antler tines are comparatively short and the bez tine is often missing (De Stefano, 1911; Abbazzi, 1995b). The condylobasal length and the upper tooth row length of the skull from Settecannelle (Central Italy) figured by Abbazzi (1995b; CBL measured from the figure is ca. 430 mm) correspond to the largest individuals of modern *C. canadensis sibiricus* (according to the data of Heptner and Zalkin, 1947). The facial part of the skull from Settecannelle is relatively short (59.5% of the CBL length) as in modern wapiti. Some remains of this endemic wapiti form are reported from the Holocene of southern Italy, however, the osteological remains ascribed to *C. canadensis* palmidactyloceros require a thorough revision since the second coeval elaphine deer *C. elaphus maral* Ogilby, 1840 (probably is a senior synonym of *C. elaphus aretinus* Azzaroli, 1961) from Italy developed rather robust crown tines that sometimes look as small palmations (De Stefano, 1911). This morphological parallelism was interpreted by Abbazzi (1995b) and Di Stefano et al. (2015) as an intraspecific variation of *C. elaphus*. However, there are some important morphological distinctions between *C. elaphus maral*/*aretinus* and *C. canadensis palmidactyloceros*: the crown part in the Italian maral is multiaxial and richly branched, while in the Alpine wapiti the crown part always consists of three main crown tines aligned in the parasagittal plane. The strongest first crown tine normally is bifurcated and this feature is rather constant in *C. canadensis palmidactyloceros* from Switzerland and Italy. The almost complete (splanchnocranium is missing) subfossil articulated skeleton of an adult male from Balkakra, Scania (Sweden) (Ahlen, 1965: fig. 9) shows a great affinity with Alpine wapiti. The antlers of Swedish wapiti are characterized by a pronounced compression from the sides above the trez tine and the typical wapiti parasagittal orientation of the crown plane. The trez tine is the strongest and the longest one. Unlike the typical form of *C. canadensis palmidactyloceros*, the wapiti individual from Sweden lacks the bifurcation of the first crown tine.

Cervus canadensis tyrrhenicus Azzaroli, 1961

Azzaroli (1961) described this dwarfed insular deer from the cave deposits of Capri (Italy) as *C. elaphus tyrrhenicus*. The body size is close to that of *C. elaphus corsicanus* and *C. elaphus barbarus*, however, the teeth are relatively larger (the lower tooth series exceeds in length the largest specimens of modern *C. elaphus* from France) suggesting a rapid and significant body size reduction. Unlike *C. elaphus corsicanus*, the metacarpal bone in *C. canadensis tyrrhenicus* is significantly shorter than the radius. The third lobe of M_3 is often reduced; P_4 is molarized; the lower premolar series is relatively short and attains 58% of the molar series length; the protocone in upper molars is supplemented with an additional enamel fold (Azzaroli, 1961: tab. 7, fig. 1) that was never recorded in *C. elaphus*. The antlers are less divergent and characterized by the presence of short brow and trez tines. The bez tine is always missing, while the distal part of the antler is extended into a small palmation terminated with three tines situated in the parasagittal plane: the stronger anterior crown tine that represents a continuation of the antler beam, and two smaller tines that have a posterior position on the main antler axis. The parasagittal orientation of crown tines in the dwarfed deer from Capri is remarkable and was noticed by Azzaroli (1961) who dedicated a part of his discussion to morphological features of wapiti. Nonetheless, according to the state of knowledge at that time, the occurrence of a dwarfed wapiti on a Mediterranean island was incredible, so Azzaroli (1961) assumed that the dwarfed deer from Capri was phylogenetically related to *C. elaphus aretinus* from the Late Pleistocene of Italy. However, *C. elaphus aretinus* is characterized by a multiaxial crown and may be very close to, or even synonymous with, C. *elaphus maral* (Croitor and Cojocaru, 2016). The fossil and subfossil remains of *C. elaphus* maral from Italy were reported by De Stefano (1911), therefore, the synonymy of *C. elaphus aretinus* and *C. elaphus* maral should not be excluded. The shape of the flattened distal portion of antlers of *C. canadensis tyrrhenicus* shows a clear affinity with the antler morphology of *C. canadensis palmidactyloceros*: the strong anterior crown tine corresponds to the strongest first crown tine in continental wapiti that represents a continuation of the antler beam; the second smaller crown tine is a homologue of the accessory prong or bifurcation of the first crown tine in *C. canadensis palmidactyloceros*. The lowermost posterior crown tine in *C. canadensis tyrrhenicus* is a simplified homologue of the distalmost part of antler in continental wapiti (second and third crown tines). This part of the antler in *C. canadensis tyrrhenicus* is reduced in size and has lost the bifurcation usually reported as the second and the third crown tines in continental wapitis. The isolation of the island population of Italian wapiti occurred during the post-glacial sea level rise.

Cervus canadensis combrayicus Croitor, 2020

This extinct form of wapiti from the Late Pleistocene of Saint-Hippolyte (Central France) is generally as large as *C. canadensis cherskii* and modern *C. canadensis sibiricus* and by 11–15% larger than *C. canadensis palmidactyloceros*. The estimated body mass of this wapiti form based on the occipital height is ca. 364 kg according to the methodology proposed by Janis (1990). The comparatively smaller antlers of the French wapiti may reflect the rather young individual age of the type specimen (Fig. 3.39). Unlike *C. canadensis mongoliae*, the wapiti from Saint-Hippolyte is characterized by a relatively shorter crown part and the relatively and absolutely longer proximal portion of the antler between the bez and the trez tines. *C. canadensis cherskii* has rather an intermediate position between the extreme forms of antler shape seen in *C. canadensis mongoliae* from one hand, and in *C. canadensis combrayicus* from another hand. Unlike both *C. canadensis mongoliae* and *C. canadensis cherskii*, the French wapiti is distinguished by the relatively small size of the first crown tine that is deviated sideward and therefore is not situated in the same parasagittal plane with the other two crown tines. The trez tine in *C. canadensis* from Saint-Hippolyte is much smaller and is directed downward, thus representing a peculiar feature of this fossil form.

Unlike modern *C. canadensis canadedsis* and closely related *C. canadensis sibiricus*, the French fossil wapiti is characterized by a much stronger divergence of antlers, the longer distance between the bez and trez tines, the downward direction of the trez tine, which is comparatively much shorter, and the weak development of the first crown tine, which is pointed more sideward and therefore deviates from the plane of other two crown tines. The difference from modern *C. canadensis xantopygus* is much deeper: besides the all above-mentioned distinctions from other modern wapitis, *C. canadensis combrayicus* is distinguished from *C. canadensis xantopygus* by curved antler beams between the bez and trez and above the trez tine. Certain parallelism may be seen in the weak development of the crown part of the antler in both *C. canadensis* from Saint-Hippolyte and *C. canadensis xantopygus*. The strongly divergent antlers of the French wapiti remind the *C. canadensis palmidactyloceros*, however, the deer from Saint-Hippolyte is distinguished from the Alpine wapiti by the lack of distal palmation, the downward direction of the trez tine, and the unbranched first crown tine.

Genus *Praedama* Portis, 1920

Synonymy:

Dolichodoryceros Kahlke, 1956

Nomenclatural acts. Portis (1920) originally proposed *Praedama* as a subgenus of the genus *Cervus* to include the large- to medium-sized deer of the Pleistocene in England and France: *Cervus falconeri* Dawkins, 1868; *Cervus savini* Dawkins, 1868; *Cervus verticornis* Dawkins; *Cervus browni* Dawkins, 1868; and *Cervus carnutorum* Laugel. This highly eclectic list of species includes fossil cervid forms that today are included in several genera. For example, *Cervus falconeri* is included in the genus *Eucladoceros* and is regarded here as a subspecies of *Eucladoceros ctenoides*. *Cervus verticornis* is included in the genus *Praemegaceros* (Kahlke, 1969; Vislobokova, 1990; Abbazzi, 2004; Croitor, 2006a). *Cervus browni* Dawkins, 1868 is a synonym of *Dama clactoniana* (Falconer, 1868), while *Cervus carnutorum* was originally based on a mixed sample that includes remains of at least two large cervid forms (Heintz and Poplin, 1980).

Azzaroli (1953) included *Cervus savini* in the genus *Megaceros* Owen, 1844 (= *Megaloceros* Brookes, 1828) and suggested that *Megaceros savini* was a primitive giant deer form related to *Megaloceros giganteus*. This opinion was shared by Caloi and Palombo (1980), Lister (1987, 1993), van der Made (2003, 2014, 2018), and van der Made and Tong (2008).

Kahlke (1956) proposed a new genus and species named *Dolichodoryceros suessenbornensis*. Later, he included *Dolichodoryceros* in the synonymy of *Praedama* (Kahlke, 1965). According to Croitor et al. (2019), the genus *Praedama* Portis, 1920 should be retained, since it reflects the particular evolutionary specialization and the specific mosaic combination of both the advanced (very obtuse mandibular angle) and primitive (unmolarized lower fourth premolar) characteristics, which differ from those seen in *Megaloceros*.

Cervus savini is recognized as the type species of *Praedama*; however, van der Made (2018) reports that the nomenclatural act designating *Cervus savini* as the type species was never completed. According to van der Made (2018), Kahlke (1965), who acted as the first reviewer of *Praedama*, did not explicitly select a type species, but only attributed both *P. savini* and *P. suessenbornensis* to this genus. Nevertheless, it should be clear from the context that *Cervus savini* is the type species of *Praedama* since this species was originally included in the genus by Portis (1920). The second species included by Kahlke (1965) in *Praedama*, *Dolichodoryceros* *suessenbornensis*, is the type species of *Dolichodoryceros*. Radulescu and Samson (1967) designated *Cervus savini* as a type species of *Dolichodoryceros*, since they regarded it as a synonym of *Dolichodoryceros suessenbornensis*, while *Cervus falconeri* Dawkins (now included in *Eucladoceros*) was proposed as a type species of *Praedama*. Indeed, the nomenclatural acts proposed by Radulesco and Samson (1967) introduced some confusion in the taxonomy of *Praedama* and are today merely of historical interest.

Diagnosis. Medium to large-sized deer. The skull is characterized by a little flexed braincase, a long orbitofrontal portion with the anterior edge of orbit downward projection that passes behind M^3, and a narrow, wedge-shaped basioccipitale. The antlers are characterized by a flattened, likely bifurcated basal tine, a middle tine that is compressed from the sides, a posterior tine, and an upright crown part that may consist of 3-4 tines. The dentition is characterized by the absence of upper canines and a primitive morphology of P_4.

Type species. *Cervus savini* Dawkins, 1885.

Locus typicus. Norfolk, Suffolk.

Stratum typicum. Forest Bed Formation.

Composition: *P. 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) (Middle Pleistocene, the Iberian Peninsula); *P. dupuisi* (Stehlin, 1912) (the final stage of Early Pleistocene, France); *P. degiulii* (Kahlke, 1997) (late Early Pleistocene, Central and Eastern Europe).

Praedama savini (Dawkins, 1885)

Synonymy:

1885 *Cervus savini* sp. nov.: Dawkins, pl. 3, fig. 3.
1920 *Cervus* (*Praedama*) *Savini* Dawkins: Portis, p. 136.
1953 *Megaceros savini* (Dawkins): Azzaroli, p. 67, Figs. 23 D, 28 K, L, 29 C, D, 37-40.
1956 *Dolichodoryceros suessenbornensis* gen et sp. nov.: Kahlke, p. 40.
1967 *Dolichodoryceros savini* (Dawkins): Rădulescu and Samson, p. 320.
1990 *Praedama savini* (Dawkins): Vislobokova, p. 161.
1990 *Praedama suessenbornensis* (Kahlke): Vislobokova, p. 161.

Nomenclatural acts. The original description of *Cervus savini* is based on fragments of antler and frontal bones from the Pleistocene deposits of the Cromer Forest Bed Formation (Dawkins, 1885). Kahlke (1956) proposed a new species, *Dolichodoryceros suessenbornensis*, based on a well-preserved antlered frontlet with complete antlers from the Middle Pleistocene at Süßenborn (Germany). The synonymy of *C. savini* and *D. suessenbornensis* has been confirmed by Radulesco and Samson (1967), Azzaroli (1979), and Lister (1993). Caloi and Palombo (1980) and Ruiz-Bustos et al. (1990) also support this viewpoint and ascribe poor remains of *Praedama* to *P. savini*. Vislobokova (1990, 2013), on the other hand, recognizes *P. suessenbornensis* as a full species. According to Vislobokova (2012, 2013), *P. suessenbornensis* differs from *P. savini* in the weaker divergence of its antlers, the narrower first tine, and various features of branching in the distal part of the antler. The diagnostic differences may represent individual and/or ontogenetic variation, while characteristics such as the relative breadth of the basal tine and the divergence of antlers are difficult to estimate, as no complete antlered skulls are known from the Forest Bed Formation, and no antler specimens with complete basal tine have been reported to date.

Description. The antler base of *Praedama savini* is square-shaped (Dawkins, 1887: pl. 3, fig. 3). This specific cross-sectional outline evolves partially as a result of the development of the flattened basal tine, given that both margins of the basal tine extend on the antler base with well-expressed ribs. The basal part of the flattened tine is set obliquely to the beam axis, while its cross-section is triangular or rhombus-shaped. The antler beam above the first tine becomes compressed in the lateromedial direction, while there is no lateral groove on the beam and the basal tine.

Almost nothing is known about the cranial morphology of *P. savini*. The obtuse angle (140°) between the horizontal and ascending parts of mandible M17537 (NHML) from the Forest Bed Formation suggests that the facial part of the skull was elongated. The correlation between the elongated face – an advanced evolutionary characteristic in cervids (Vislobokova, 1990) – and the obtuse angle between the ascending and horizontal parts of the mandible characterizes, for example, the modern red deer. The mandibular angle in giant deer *Megaloceros giganteus* is much narrower (105° in the specimen M2328, NHML) and indicates more primitive cranial proportions with a relatively shorter splanchnocranium (or orbitofrontal segment of splanchnocranium) than in *P. savini*, thus ruling out a direct evolutionary relationship between these two cervid species.

It is unclear whether the Middle Pleistocene remains from the Iberian Peninsula reported as *P. savini* are the same form as *Praedama* from Süßenborn and the Forest Bed Formation or should be regarded, at least, as a different subspecies. The virtually complete antler of *Praedama* from Pinedo, reported tentatively by Martin Aguado (1962) as *Eucladoceros*, shows a more complicated and richly branched crown with a comb-like pattern reminiscent of *Eucladoceros*, but quite distinct from the simple three-tined crown of the well-known specimen from Süßenborn (Kahlke, 1956: pls. 15-16). The general bauplan of *Praedama* antler from Pinedo corresponds to the antler bauplan of *M. giganteus*.

Distribution. The Middle Pleistocene of the Tiraspolian Gravel (Moldova) has yielded easternmost remains attributed to *P. savini*, as reported by Kahlke (1971). The richest and most diverse paleontological record of *Praedama* in Europe comes from the Iberian Peninsula, where remains of *P. savini* have been identified at several Middle Pleistocene sites (Andres and Aguirre, 1974; Kahlke, 1971; Ruiz-Bustos et al., 1990). In addition, a well-preserved shed antler (IPS13370) from the D7 layer of Cal Guardiola (Terrassa, Northeast Iberia) reported by Madurell-Malapeira et al. (2010) as *Praemegaceros verticornis* actually belongs to *Praedama*.

Praedama novocarthaginiensis (van der Made, 2014)

Synonymy:

1981 *Megaceros (Megaceros) savini* (Dawkins): Carbonell et al., p. 50, figs 4-5.

2014 *Megaloceros novocarthaginiensis* sp. nov.: van der Made, p. 276, figs. 3-16.

Nomenclatural acts. The fossil remains from the Early-Middle Pleistocene of Cueva Victoria were initially identified as *Praedama savini* by Carbonell et al. (1981). However, later research by van der Made (2014) established a new species, *Megaloceros novocarthaginiensis*, based on the *Praedama* material from this site. According to van der Made, the new species comes from the latest Early Pleistocene and can be distinguished from *P. savini* by its larger size, higher position of the basal tine, and lower degree of mandibular pachyostosis.

Diagnosis. The body size is larger than in genotype species. The basal tine of antler has a higher position than the type species. Metapodials are relatively short.

Locus typicus. Cueva Victoria, Spain.

Stratum Typicum. The late Early Pleistocene deposits of Cueva Victoria.

Description. Van der Made (2014) used differential diagnostic characters, such as size difference and height of the basal tine, but these may represent intraspecific individual variation. The height of the basal tine position in the specimens described by van der Made (2014) is quite variable. However, the measurements of the type specimen CV-BL1-250+251, including the height of the basal tine, match perfectly with those of the pedicles and basal portions of antlers of the antlered frontlet M6301 from the Forest Bed of East Runton, Norfolk. Therefore, the synonymy of *M. novocarthaginiensis* with *P. savini* is quite probable if one takes into account the diagnostic characteristics reported by van der Made (2014).

As for mandibular pachyostosis, there is no clear evidence of its particular development in *P. savini*. This is because the mandibles tentatively ascribed to this species are not directly associated with antlers (Azzaroli, 1953), and thick mandibles of medium-sized cervids that might be associated with the antlers of *P. savini* from the Forest Bed Formation or Süßenborn are unknown. For example, the aforementioned mandible M17537 from the Forest Bed Formation does not present any unusual degree of thickening of its horizontal ramus that might be considered pachyostosis.

Praedama dupuisi (Stehlin, 1912)

Synonymy:

1912 *Cervus* (*Megaceros*) *dupuisi* sp. nov.: Stehlin, p. 201, pl. V, figs. 10, 11.
1953 *Megaceros dupuisi* (Stehlin, 1912): Azzaroli, p. 52.
1997 *Eucladoceros giulii* sp. nov. (partim.): Kahlke, p. 229, fig. 26.
2003 *Peaemegaceros verticornis* (Dawkins): Guerin et al., p. 71, fig. 9.
2004 *Arvernoceros giulii* (Kahlke, 1997): Croitor and Kostopoulos, p. 149, fig. 10.
2018 *Rucervus* (*Arvernoceros*) *giulii* (Kahlke, 1997): Croitor, p. 4.

Nomenclatural acts. This cervid form was originally described by Stehlin (de Grossouvre and Stehlin, 1912) as a megacerid species. However, the publication did not receive much attention. According to Stehlin (as cited in Bonifay, 1971), *Megaceros dupuisi* is also present in the fauna from Saint-Prest. Guerin et al. (2003), who revised the fauna from Saint-Prest, considered *Megaceros dupuisi* a junior synonym of *Praemegaceros verticornis*. The species name *Cervus* (*Megaceros*) *dupuisi* Stehlin, 1912 is available and cannot be declared a *nomen oblitum* since it has been used continuously (Azzaroli, 1953; Bonifay, 1971).

Diagnosis: a large-sized deer similar in size to modern wapiti. Pedicles are cylinder-shaped and moderately divergent. Antlers are characterized by the high position of flattened bifurcated first tine with an oblique orientation of its transversal axis. P_4 is primitive and unmolarized. Mandibles show a weak or moderate pachyostosis.

Holotype: mandible figured by Stehlin (1912)

Locus typicus: Rosieres, Cher Department, France.

Stratum typicum: sand deposits of Rosieres Quarry, Early Pleistocene.

Description. A fragment of the skull with the proximal fragment of the right antler SPP-66 (MNHN) from a large deer found in Saint-Prest, France (MNQ20, ca. 1.0 Ma), was initially identified as *Praemegaceros verticornis* (Guerin et al., 2003). However, unlike *P. verticornis*, the specimen SPP-66 has concave frontal bones, cylindrical pedicles with a circular cross-section (*dx* DLM×DAP = 75.0×66.8 mm), lacks bony burelets on the median side of the pedicle base, and has an oval cross-section of the first tine situated on the anterior side of the antler beam. The mandible SPR-73 (*dx*) shows a primitive unmolarized P_4 with a small enamel islet between the parastylid and paraconid, as seen in the large deer from Apollonia. The horizontal ramus of the mandible is rather robust, showing an early stage of pachyostosis evolution.

Another large-sized deer from the Late Villafranchian fauna of the Vallonnet Cave (South France) was also reported as *Praemegaceros* cf. *verticornis* (Moulle et al., 2006). The deer from Vallonnet is characterized by a simple P_4, vestigial cingulum in upper molars, and small protoconal fold observable in little worn molars. Antlers are robust (DAP of antler base in specimens Nr. 132 and Nr. 368, RMPM, is 69.6 mm and 65.0 mm, respectively), characterized by the high position of basal tine (101.3 mm in the specimen Nr. 132) and the strong bending of the beam toward the posterior at the level of the first ramification

Praedama giulii (Kahlke, 1997)

Synonymy:

1997 *Eucladoceros giulii* sp. nov.: Kahlke, p. 225, tab. 40, 1-6.

2004 *Arvernoceros giulii* (Kahlke, 1997): Croitor and Kostopoulos, p. 149, fig. 10.

Diagnosis. A very large deer with long and thin limb bones. The braincase is a little flexed and the orbitofrontal portion of the skull is elongated: the anterior edge of orbits is situated more caudally than the posterior edge of M^3. Mandibles are characterized by weak pachyostosis. Upper canines are missing. The lower fourth premolar (P_4) is primitive. Basal tine is flattened and bifurcated. The middle tine is long and straight. The crown part of the antler is comb-shaped.

Locus typicus: Untermassfeld (Germany).

Stratum typicum: the late Early Pleistocene deposits of Untermassfeld.

Description. The large deer from Untermassfeld had a body mass of approximately 400 kg and is characterized by a relatively primitive dentition with long lower premolars, simple unmolarized P_4, and extremely long limb bones (Kahlke, 1997). Although antler material from Untermassfeld is represented by poor fragments, one complete juvenile antler has been found with a flattened bifurcated basal tine and a distal bifurcation. Kahlke (1997) proposed a hypothesized reconstruction of the antler based on available fragments, including a distal fragment that was interpreted as a comb-like crown of *Eucladoceros*. However, the juvenile antler from Untermassfeld does not recall any ontogenetic stage of development in comb-antlered *Eucladoceros*, while the details of dental morphology and some cranial features suggest an evolutionary divergence between *E. ctenoides* and the deer from Untermassfeld that share only the basic for Cervinae primitive characters. The strong flattened and bifurcated basal tine of *Praedama giulii* that shows its strong development at the earliest stages of ontogenetic development is rather reminiscent of the antler shape of *R.* (*Arvernoceros*) *verestchagini* David, 1992 from the Early Pleistocene of southeastern Europe (Croitor and Kostopoulos, 2004). Breda et al. (2020) published a figure of the complete female skull QW 1992/23910 from Untermassfeld, which reveals interesting morphological characteristics indicating the systematic position of *P. giulii*. Unlike *Eucladoceros* and *R.* (*Arvernoceros*), the upper canines are missing in *P. giulii*. Additionally, the basioccipital is rather narrow, not bell-shaped as in *Eucladoceros*. The orbitofrontal portion is rather long, with the anterior edge of the orbit situated above the caudal edge of M^3, as predicted for *Praedama savini*. The nasal bones are moderately long and reach the imaginary line connecting the anterior edges of the orbits. The braincase is slightly flexed, and its relative length is equivocal but somewhat longer than in *Eucladoceros*, with the distance between bregma and inion (= opisthocranion) in specimen QW 1992/23910 roughly equal to the braincase breadth. Unlike *Eucladoceros*, the antlers of *P. giulii* do not possess the supplementary prong in the area of basal ramification. According to Breda et al. (2020), the flattened basal tine of antlers from Untermassfeld is reminiscent of *P. savini*. It is noteworthy that the distal "comb-like" fragment of antler IQW1982/18587 from Unretmassfeld (Kahlke, 1997) is very similar to the crown part of the antler from Pinedo (Aguado, 1962). Therefore, one could argue that the large deer forms from Untermassfeld and Pinedo belong to closely related species or even the same species.

Comments. Based on the extremely large size of postcranial bones, Kahlke (1997) and van der Made (1998, 1999) attributed all the late Villafranchian large deer remains from Atapuerca and Venta Micena in Spain, Würzburg-Schalksberg in Germany, Apollonia in Greece, and Akhalkalaki in Georgia to this peculiar long-limbed large-sized species.

Distribution. Late Early Pleistocene (Epivillafranchian) of Europe (France, Germany, Moldova).

Praedama matritensis (van der Made, 2019)

Synonymy:

2019 *Megaloceros matritensis* sp. nov.: van der Made, p. 116, fig. 3.

Diagnosis: The species has a body size similar to that of modern red deer from the Iberian Peninsula. The pedicles and antlers exhibit strong divergence. The mandibles are pachyostotic, and the upper molars lack cingulum. The lower fourth premolar (P_4) is unmolarized.

Locus typicus: the Manzanares Valley (Madrid Area, Spain).

Stratum typicum: the Middle Pleistocene deposits of the Manzanares Valley.

Description. *Praedama matritensis* is primarily diagnosed based on well-preserved mandibles and lower teeth morphology, as well as its relatively small size (van der Made, 2019). The mandibles of this species exhibit a remarkably inflated horizontal ramus, which van der Made (2018) correctly described as pachyostotic, as well as a strongly convex lower margin, an obtuse mandibular angle (130°), and the primitive morphology of P_4 (van der Made, 2019: Fig. 6). Although the validity of this species is not in question, some of the postcranial elements attributed to it may actually belong to a larger cervid form.

The pachyostosis of the mandible in *P. matritensis* is an intriguing morphological and paleobiological characteristic that requires special attention. All mandibles of *P. matritensis* exhibit pachyostosis, which thus represents a stable specific character of this cervid form (van der Made, 2019).

Pachyostosis in ruminants is considered by Morales et al. (1992) to be an adaptive physiological response to environmental change. The pachyostotic parts of the skeleton act as "bone sinks", where excess bone tissue can be stored during seasons of abundant nutritious vegetation. In cervids, cranial pachyostosis represented a similar secondary metabolic response to environmental factors, primarily low primary ecological production and marked seasonality (Morales et al., 1992; Croitor, 2016). The relatively dry or even arid environmental conditions of certain Pleistocene Iberian sites, including Venta Micena (sclerophyllous woodlands), Atapuerca (steppes), and Huescar 1 (deserts), were reported by Hernandez Fernandez et al. (2006). Therefore, the unusual mandibular pachyostosis observed in *P. matritensis* could be attributed to arid climate pulses during the Pleistocene that shaped the specific conditions of local evolutionary processes. Mandibular pachyostosis has only been described in members of the subfamily Cervinae and does not correlate with body size or relative antler size. It has been observed in small *Sinomegaceros robustus* (the size of modern roe deer) from the Late Tertiary in Kazakhstan, large *Megaloceros giganteus* from the Middle and Late Pleistocene in mid-latitudes of Eurasia, and medium-sized *Megaceroides algericus* from the Late Pleistocene in North Africa (Croitor, 2016). The only characteristic these species share is their occurrence in extreme peripheral regions of the distribution area of the subfamily Cervinae (i.e., arid zones of Central Asia and North Africa and the plains of Eurasia with dry continental climate), where they would have been exposed to stressful environmental conditions, including seasonal (or perhaps even irregular) declines in forage supply. Thus, additional mineral deposits in the pachyostotic bones would have been strategically important for their survival. It can be assumed that *P. matritensis* from the Middle Pleistocene in the Iberian Peninsula evolved mandibular pachyostosis in similarly arid environmental conditions combined with regular or irregular declines in vegetation forage supply. It should be emphasized that the Iberian *P. matritensis* may be considered a paleobiogeographic counterpart of the North African *M. algericus*, which also evolved a remarkable degree of cranial and mandibular pachyostosis (Croitor, 2016).

Genus *Leptocervus* Capasso Barbato, 1990

Nomenclatural acts: *Leptocervus* was first introduced as a subgenus of *Cervus* in the Mediterranean insular deer overview by Capasso Barbato (1990). The original publication did not provide a diagnosis and type species designation. From the publication, it is clear that Capasso Barbato (1990) included three endemic species from the Late Pleistocene of Crete in the composition of *Leptocervus*: *Candiacervus rethymnensis* Kuss, 1975, *Cervus major* Capasso

Barbato and Petronio, 1986, and *Cervus* (*Leptocervus*) *dorotensis*, which was named for the first time. Later, Capasso Barbato (1992) published a formal diagnosis of *Leptocervus* and designated *Cervus* (*Leptocervus*) *major* as the type species. It is worth noting that the species name *Cervus major* Capasso Barbato and Petronio, 1986 is likely invalid as it is a primary homonym of several earlier species names, which are, however, not in use in most cases. These include *Cervus axis major* Kerr, 1792, *Cervus mantschuricus major*, *Cervus major* Ord, 1815 (a junior synonym of *Cervus canadensis*), and *Cervus* (*Subulo*) *simplicornis major*, Wagner, 1855. For further details, refer to Lydekker, 1915.

Composition: *Leptocervus major* (Capasso Barbato and Petronio, 1986) (Crete, Late Pleistocene), *Leptocervus dorotensis* Capasso Barbato, 1990 (Crete, Late Pleistocene).

Leptocervus dorothensis Capasso Barbato, 1990

Nomenclatural acts: the relatively large cervid from the Grotto of Bate was first reported by Capasso Barbato (1990) as *Cervus* (*Leptocervus*) *dorothensis*. The original publication contains a figure of a complete and well-preserved metatarsal bone ascribed to the cervid form in question and a brief characterization of the species. However, the original description does not provide a formal diagnosis of the new species. Capasso Barbato (1990) suggested that the new species is closely related to *Cervus rhenanus* Dubois and *Cervus pelloponesiacus* Sickemberg, and placed the Cretan deer in the subgenus *Leptocervus* to emphasize its endemic character. Later, Capasso Barbato (1992) redescribed the species in question, providing a diagnosis ans specifying the distribution, type level, and type specimens. Capasso Barbato (1992) designated the right radius Nr. 25 as a holotype. The author also designated a series of paratypes, including the left metatarsal Nr. 36 (*ibidem*: fig. 5, h, j), which is likely figured in the first publication where the species name appeared for the first time. Therefore, the left metatarsal Nr. 36 is the holotype. The antler and craniodental remains of the species are still unknown, leaving its systematic position unclear. Schilling and Roessner (2021) included the species in the genus *Candiacervus*, but since the relationship of *Leptocervus dorothensis* to *Candiacervus* cannot be demonstrated, the genus name *Leptocervus* is maintained here.

Diagnosis. A rather large deer similar in size to *Eucladoceros* and ca 20 % smaller than the type species *Leptocervus major*. Metapodials are elongated and slender. The length of the metatarsal attains 315 mm. The distal epiphysis of the metatarsus is somewhat inflated, but in lesser degree than in *L. major*.

Holotype: a complete left metatarsal Nr. 36 (Capasso Barbato, 1990: fig. 2, the second specimen from the right; 1992: fig 5, h, j).

Locus typicus: Bate Cave, Crete, Greece.

Stratum typicum: the Upper Pleistocene deposits of the Bate Cave.

Description. The metatarsal from Bate Cave is similar in size to *Eucladoceros ctenoides* and *Rucervus radulescui*, but it has a distinct morphology. The metacarpal of *C. dorothensis* is slender and characterized by a specific inflation of the distal part of the diaphysis, which terminates with a narrow epiphysis. Unlike *R. radulescui*, the condyles of the distal epiphysis are poorly expressed. The remarkably elongated metapodials of *L. dorothensis* suggest a possible phylogenetic relationship between this insular deer and continental *Praedama degiulii* (Kahlke, 1997) from the final stage of the Early Pleistocene in Untermassfeld, Germany. Both *L. dorothensis* and *P. degiulii* are characterized by elongated metapodials, which represent one of their main diagnostic features (Kahlke, 1997). However, the possible relationship between *L. dorothensis* and *P. degiulii* requires further investigation.

Genus *Megaloceros* Brookes 1828

Nomenclatural acts. The traditional view of *Megaloceros* encompasses all giant Cervinae forms from western Eurasia, including their supposed smaller ancestors and insular dwarfed descendants (Azzaroli, 1953, 1979; Lister, 1994). However, this concept is no longer widely accepted, as it has become clear that the group of giant deer is better understood as comprising several independent lineages that share similar eco-morphological characteristics, but are phylogenetically distant from each other (Vislobokova, 1990, 2012; Croitor, 2006a).

Type species: *Alce gigantea* Blumenbach, 1799.

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

Megaloceros giganteus (Blumenbach, 1799)

Synonymy:

1799 *Alce gigantea* [sp. nov.]: Blumenbach, p. 197.

1822 *Cervus hibernus* [sp. nov.]: Desmarest, p. 446.

1825 *Cervus megaceros* [sp. nov.]: Hart, p. 23, pls. I-III.

1827 *Cervus* (*Dama*) *giganteus* (Blumenbach, 1799): Cuvier, p. 306.

1828 *Megalocerus antiquorum* [sp. nov.]: Brookes, p. 61.

1830 *Cervus euryceros* (Aldrovandi, 1621): Hibbert, p. 301, pl. III, fig. 9.

1834 *Cervus euryceros irlandicus* [ssp. nov.]: Fischer, p. 160.

1838 *Cervus megalocerus* (Hart, 1825): Fischer, p. 534.

1844 *Cervus* (*Megaceros*) *hibernicus* [sp. nov.]: Owen, p. 237.

1846 *Megaceros hibernicus* (Owen, 1844): Owen, p. 444, fig. 182.

1892 *Cervus* (*Euryceros*) *hiberniae* (Owen, 1844): Pohlig, p. 217, fig. 1, 2.

1929 *Cervus giganteus* (Blumenbach): Reynolds, p. 1.

1935 *Megaceros euryceros latifrons* ssp. nov.: Raven, p. 178, fig. 1-13.

1953 *Megaceros giganteus* (Blumenbach, 1799): Azzaroli, p. 48.

1962 *Megaloceros giganteus* (Blumenbach, 1803): Godina et al., p. 374, fig. 496.

1987 *Megaloceros giganteus* (Blumenbach, 1799): Lister, p. 255.

2006 *Megaloceros giganteus irlandicus* (Fischer, 1834): van der Made, p. 125, fig. 10.

Nomenclatural acts. Cuvier (1823: p. 72, tab. VII: figs. 1, 2, 3, 4) provided a quite detailed description and measurements of the skull from the “Royal Cabinet” (now Musée nationale d’histoire naturelle in Paris; the specimen was donated by Colonel Thornton). Cuvier (1823) proposed to consider this specimen as a type of *Megaloceros giganteus* (neotype according to the rules of the International Code of Zoological Nomenclature). Thus in the absence of the original material, this specimen may be regarded as a neotype. Hibbert (1830) proposed to use the species name *Cervus euryceros* taken from Aldrovandi’s interpretations of antique texts. This name has been used in old publications for the designation of the "continental" forms of giant deer. Nonetheless, Aldrovandi’s “c*ervus euryceros*” is unavailable, since according to Article 3.2 of the International Code of Zoological Nomenclature no name published before 1758 enters zoological nomenclature (Berckhemer, 1941).

The type specimen of *Megaloceros giganteus* used by Blumenbach (1799) for the species description remained unknown for a long time (van der Made, 2006). The original Blumenbach’s (1799: 697) description of *Alce gigantea* provides quite scanty information about the species, specifying only that this particular kind of “fossil elk” comes from Ireland and is characterized by immense body size. The skull of giant deer is almost an ell long and the distance between summits of antlers may attain 14 feet (ca. 4.3 m) (Blumenbach, 1799). The original description does not provide any reference. Blumenbach (1799) specifies in a quite imprecise way the type locality (Ireland) and provides only two measurements, the skull length and the antler span. Nonetheless, the available information is sufficient and allows the identification of a specimen with the quoted characteristics. The publication of Blumenbach was preceded by only five reports of giant deer findings from Ireland that are enlisted here in chronological order: 1) the antlered skull from Dardistown near Drogheda (Molyneux, 1697); 2) the shed antler found near Downpatrick, North Ireland (Kelly, 1727); 3) the antlered skull found near Dunleer, Ireland (Wright, 1748); 4) the antler found in 1783 near Dromore, County Down, North Ireland (Cuvier, 1823); and 5) the antlered skull found near the Nobber Village, Ireland (Razoumowsky, 1786). The antlered skull from Dunleer environs that Wright (1748) studied when he visited Barmeath Castle represents a particular interest, since its measurements—namely the unusually large distance between the antler summits—fully correspond to the antler span measurement quoted by Blumenbach (1799). Therefore, following Articles 72.4.1.1 and 72.4.5 of the International Code of Zoological Nomenclature, the antlered skull from Dunleer environs is designated here as the holo-type of *Megaloceros giganteus* (Blumenbach, 1799). Apparently, Blumenbach (1799) was aware of other specimens discovered in Ireland at that time and they potentially may be considered as paratypes. However, we have no indications of which other specimens were known to Blumenbach (1799). The holotype of *Megaloceros giganteus* is currently exposed in Barmeath Castle near Dunleer, County Louth (Ireland). The area where the type specimen of giant deer was discovered should be considered as the type locality of *M. giganteus* (Blumenbach, 1799).

Holotype: antlered skull from Barmeath Castle figured by Wright (1748).

Locus Typicus: environs of Dunleer, Ireland.

Stratum typicum: the Late Pleistocene of Ireland.

Description. The material from Ireland shows a meaningful split in metacarpal length and robustness. The metacarpals of mounted skeletons of the female exposed in the Paleontological Gallery of Paris, the male from the Natural History Museum "Grigore Antipa" of Bucharest, the male from Athlone (Ireland), the male from an unidentified Irish site exposed in the Museum of Nature of Wroclaw, and the skeleton from Enniscorthy (Ireland; stored in the Sedgwick Museum of Cambridge) described by Reynolds (1929) are short and relatively robust, overlapping with the sample from Bruine Bank (Croitor et al., 2014). The metacarpals of the mounted male skeletons from the Paleontological Gallery of Paris and the Paleontological Institute of Munich are particularly long approaching the giant deer from Schlutup (Germany) and Sapozhok (Russia). This group of specimens corresponds to van der Made's (2006) Late Devensian group of "intermediate type of metapodials". Regarding the relative length of the upper premolar series, the sample from Ireland again is divided into two groups: the small group of specimens with relatively long premolar series that overlap with the main part of the sample from the Rhine basin, North Kazakhstan, and the specimen from Brînzeni-1 (Moldova), and the group with relatively short premolar series that may be approached to the larger specimen from Sapozhok (Croitor et al., 2014). It is difficult to confirm the relationship between the limb proportions and the tooth series proportions taking into consideration only the mounted skeletons of giant deer from Ireland, since those showpieces originally were subjects of commercial selling and we don't know if the skeletons are genuinely articulated, or (what is more probably) compiled. Therefore, it is very difficult to define the "typical Irish" subspecies *M. giganteus giganteus*, since the material from Ireland includes both the "robust" and "long-limbed" types of giant deer. Van der Made (2006) and Lister (1994) regarded the "typical" giant deer from Ireland as one of the most long-limbed forms.

According to van der Made (2006), the relatively slender Irish form of giant deer arrived in Western Europe 10-13 Ka from Eastern Europe.

The skeleton of giant deer from Sapozhok (Ryazan, Russia) stored in the Paleontological Institute, Moscow (collection number PIN-337) is a genuinely articulated skeleton that is important for our understanding of the Irish material. This is a long-limbed large form characterized by the antler shape as in *M. giganteus* from Ireland, the well-developed cingulum in upper molars, and the particularly short premolar series, thus suggesting the association of long limbs with short premolar series (Croitor et al., 2014). The presence of large long-limbed giant deer with advanced dentition in Eastern Europe supports the hypothesis of van der Made (2006) on the immigration of the "classical Irish" form of *Megaloceros giganteus* from the East around 13 ka. The older remains of giant deer are described as several subspecies distinguished mostly by their antler morphology.

Subspecies:

Megaloceros giganteus antecedens Berckhemer, 1941 from the Holsteinian of Steinheim, Germany (ca. 400 or 300 kyr BP), is the oldest giant deer form in Europe that is considered as a primitive forerunner of *M. giganteus ruffii* and *M. giganteus giganteus* (Azzaroli, 1953; van der Made, 2003; Vislobokova, 2012). Azzaroli (1953) granted Berckhemer's giant deer the full specific rank because of the remarkable shape of its antlers. The antlers of *M. giganteus antecedens* are most deviant if the Irish giant deer is regarded as a "typical" form: the basal tine in the deer from Steinheim is transformed into a broad plate-shaped palmation, the middle tine adjoined the distal antler palmation, the crown tines are inserted on anterior and distal sides of palmation, while the posterior tine is very large and flat, therefore the general shape of the distal part of the antler is rather elk-like. Kahlke (1999) noticed a conspicuous morphological affinity of *M. giganteus antecedens* with *Sinomegaceros pachyosteus* from Zhoukoudian and explained this affinity as a morphological parallelism in similar ecological circumstances. This subspecies is characterized by the long nasal bones that extend behind the anterior orbital line, the small but visible preorbital fossae, and elongated distal portions of limbs. The cingulum in the upper molars is not developed.

Megaloceros giganteus ruffii Nehring, 1891 from Kottbus area (Germany) characterized by the smaller antler span, the broader palmation and the crown tines inserted on the distal edge of the palmation (not on the anterior side as in Irish giant deer). The antlered skull Nr. 6517.5.9.73.4 from Bruhl (SMNH) ascribed to this subspecies (Vislobokova, 2012) is characterized by rather large and deep preorbital fossae, closed ethmoidal orifices, smooth and irregularly rounded *bullae tympani*, and protruding orbits. The cingulum in the upper molars is not developed.

Megaloceros giganteus germaniae Pohlig, 1892 is characterized by a more compact antler crown, and a frontal orientation of palmations, which become more visible during the frontal visual contact of their bearer with a rival. Its antler crowns are strongly bent medially and toward the posterior, the middle tine normally is separated from the palmation.

Megaloceros giganteus italiae Pohlig, 1892 is generally characterized by a similar type of antler shape, as *M. giganteus ruffii* and *M. giganteus germaniae*, however, its medial tine often adjoins the distal palmation (Pohlig, 1892). According to van der Made (2006) and Vislobokova (2012), the subspecies names *ruffii*, *germaniae* and *italiae* are synonymous. Possibly, the Italian giant deer should be maintained as a separate subspecies, since the antlered skull IGF11630 (MGUF) is very distinct from the Irish, German, and East European samples in its relatively broad braincase: the index DNr/LBr in the skull from Tuscany is 129.9%, while in the lumped data for Irish and German samples varies between 85.4% and 101.1% (Croitor, work in progress).

Van der Made (2006) distinguished in the sample from the Rhine basin and the North Sea two morphological forms of giant deer: the older Holsteinian/Hoxnian and Saalian/Wolstonian *M. giganteus* "*antecedents*/*germaniae*" with slender metacarpals, and younger Eemian *M. giganteus ssp.* with robust metacarpals. The majority of findings from Poland, Ukraine, and Moldova belong to the giant deer form characterized by the relatively long upper and lower premolar series and the vestigial or missing cingulum in upper molars. This form of giant deer is close to the "robust type" described by Lister (1994) and van der Made (2006). The giant deer from Biśnik Cave (70–60 ky BP; Poland) seems to be close to *M. giganteus ruffii*, but a definite conclusion is not possible, since antlers of the Polish form are not known. The female skull of the giant deer from Biśnik Cave is characterized by the shallow, but clearly outlined preorbital fossae (their depth is 5.5 mm), the short nasal bones that do not reach the imaginary line connecting the anterior edges of orbits, the weak development of cingulum in upper molars, and the rather short massive metacarpus, which is somewhat smaller than the metacarpal bone found in the association with the type specimen of *M. giganteus ruffii* (Croitor et al., 2014). It is difficult to classify the shape of the metacarpal from Biśnik as robust or slender since it is characterized by a relatively narrow distal epiphysis and a rather massive shaft. The lower mandibles from Biśnik are characterized by the relatively long premolar series (61.9-65.6%, n=3) and stand closer to large individuals of the sample from the Rhine Bassin stored in SMNH.

Megaloceros mugharensis (di Stefano, 1996)

Synonymy:

1996 *Dama clactoniama mugharensis* ssp. nov.: di Stefano, p. 304, figs. 3, 4.

Diagnosis: A middle-sized cervid with relatively short and robust limb bones. The basal tine of the antler is flattened and bifurcated. The antler becomes flattened in the area of the middle tine. Upper molars are supplemented with a weak cingulum. The lower premolar series is relatively long and attains 66% of the molar series length. The lower fourth premolar is molarized.

Locus typicus: Tabun, Israel.

Stratum typicum: the Middle Pleistocene deposits of Tabun.

Description. The remains of this medium-sized deer are highly fragmented but nonetheless interesting. The antlers are characterized by a strong bifurcated, flattened basal tine located near the burr. The angle between the basal tine and the beam is obtuse. The proximal section of the antler beam is flattened, and a variable middle tine is situated around 10-15 cm from the burr (Di Stefano, 1996). Di Stefano (1996) described *Dama clactoniana mugharensis* from the Middle Pleistocene of Tabun E, Middle East, as a transitional form between *Dama clactoniana* from the Middle Pleistocene of Europe and modern *Dama mesopotamica*. However, this assumption is unlikely since *D. clactoniana* typically features a simple, cylinder-shaped basal tine and does not develop flattened bifurcated variants, although supernumerary and even bifurcated crown and middle tines are common in this species (Leonardi and Petronio, 1976). The antlers of *D. mesopotamica*, on the other hand, are characterized by a significantly reduced size of the basal tine, indicating an evolutionary specialization opposite to that of *Megaloceros mugharensis*.

In my opinion, the flattened bifurcated basal tine situated near the burr and the obtuse angle of the first ramification bring the cervid from Tabun closer to *M. giganteus*. Di Stefano (1996) also reported a comparatively strong development of basal structures in the upper molars (entostyle and the "anterior and posterior cingulum"), which correspond to the frequent development of the cingulum in *M. giganteus*. The lower premolar series appears to be relatively long (66%, based on photographs in Di Stefano, 1996) and represents a primitive condition similar to the primitive form of *M. giganteus* from Rhine Bassin. The combination of antler morphology and the length of the premolar series is significant for the systematic classification of this cervid. The relatively long premolar series of *M. mugharensis* is more primitive than that of *D. clactoniana* from Riano (the premolar/molar index is 58.3%) and is still more primitive than Early Pleistocene *Dama vallonnetensis* from Capena (the premolar/molar index is 58.1%) and Pirro Nord (56.8%). Therefore, the long premolar series of *M. mugharensis* eliminates the possibility of a close relationship between this deer and the Pleistocene fallow deer. Limb bones are described as squat (radius length is approximately 215–220 mm and mid-shaft breadth is around 29 mm; Di Stefano, 1996: fig. 8), indicating a body size reduction similar to that of *C. elaphus rianensis*.

Based on these characteristics, it can be assumed that the medium-sized cervid from the Near East is a dwarfed primitive form of the giant deer *Megaloceros mugharensis* (Di Stefano, 1996). It is possible that *M. mugharensis* and *M. giganteus antecedens* belong to the earliest dispersal event of giant deer into the western Palearctic.

Genus *Megaceroides* Joleaud, 1914

Nomenclatural acts. Joleaud (1914) created the subgenus *Megaceroides* within the genus *Cervus* for an endemic odd cervid *Cervus algericus* Lydekker, 1890 (=*Cervus pachygenys* Pomel, 1893) from North Africa to underline its assumed archaic character and transitional systematic position between *Megaloceros* and *Dama*. Arambourg (1932, 1938) reported some new important findings of cervid cranial remains from the Late Pleistocene of Algeria (Guyotville) and Morocco (Ain Tit Mellil) that permitted him to elevate *Megaceroides* to the genus level. Joleaud (1914) stressed the affinity between *M. algericus* and the European giant deer, assuming for the African form an intermediate position between *Megaloceros* and *Dama*. Azzaroli (1953) divided all giant deer into two phylogenetic branches: the "*Megaceros giganteus* group", which also included Asian *Sinomegaceros* regarded as the terminal evolutionary branch of this group, and the "*Megaceros verticornis* group" with *M. algericus* associated with "*M*". *verticornis* and other related forms. Ambrosetti (1967) gave the formal taxonomical status to Azzaroli's informal groups: he divided the genus *Megaceros* Owen, 1843 (junior synonym of *Megaloceros* Brookes, 1828) into subgenera *Megaceros* (Azzaroli's "*giganteus* group"), and *Megaceroides* ("*verticornis* group"). The assumed close phylogenetic relationship between *Megaceroides algericus* and *Praemegaceros verticornis* was based on a single morphological character: the flattened frontal bones (Azzaroli, 1953, 1979; Ambrosetti, 1967). The detailed study of the cranial and dental morphology of *Megaceroides algericus* revealed its deep evolutionary specialization and the significant morphological and phylogenetic remoteness from *Praemegaceros verticornis* and other allied *Praemegaceros* forms (Croitor 2004, 2006a).

Megaceroides algericus (Lydekker, 1890)

Synonymy:

1890 *Cervus algericus* sp. nov.: Lydekker, p. 602, fig. 1.

1892 *Cervus pachygenys* sp. nov.: Pomel, p. 213.

1893 *Cervus pachygenys* (Pomel): Pomel, p. 35, pl. VII, figs. 1-7, pl. VIII, figs. 1-4.

1914 *Cervus* (*Megaceroides*) *algericus* Lydekker: Joleaud, p. 737.

1938 *Megaceroides algericus* (Lydekker): Arambourg, p. 33, fig. 8.

1953 *Megaceros algericus* (Lydekker): Azzaroli, p. 47, p. 51.

1967 *Megaceros* (*Megaceroides*) *algericus* (Lydekker): Ambrosetti, p. 272.

1990 *Megaceros* (*Megaceroides*) *algericus* (Lydekker): Hadjiouis, p. 249, figs. 1-4.

2010 *Megaloceros algericus* (Lydekker): Gentry, p. 813.

Holotype: the left maxilla with P^3-M^3 (Lydekker, 1890; figured on page 602), P^2 is destroyed, while M^2 and M^3 are damaged; the cast is stored at the Natural History Museum of London (Lydekker, 1890: p. 604), its collection number is M10647 (Gentry, 2010). The length of the upper molar series M^1-M^3 amounts to 58.5 mm (measured from the figure). The location of the original fossil specimen is unknown. The holotype is characterized by the strong development of a basal enamel cingulum in the upper molars.

Type locality and horizon: Late Pleistocene from Hammam Meskoutin, Guelma (Algeria).

Diagnosis: A cervid species of medium size, slightly larger than modern fallow deer and smaller than red deer. The skull is very broad: the skull breadth attains more than 60% of the condylobasal length. Splanchnocranium is relatively short: the length measured from the anterior edge of the orbits to the prosthion makes it shorter than 1/2 of the condylobasal length. Skull bones with exception of zygomatic arches are very thick. The braincase is moderately flexed: the angle between parietal bones and face profile amounts to ca. 135°; parietal bones are flat. Pedicles are moderately long (their length approximately equals their transversal diameter), deflected sideward and somewhat backwards. Frontal bones are flat and very broad. Orbits are comparatively large; their anterior edges lay at the level between M^2 and M^1. Ethmoidal vacuities are completely closed. Preorbital fossae are not developed. Basioccipitale is broad and bell-shaped. Upper canines are missing. The cingulum in upper molars is variable: it may be well-developed, or almost completely missing. The lower fourth premolar (P_4) is molarized: its metaconid is fused with the paraconid. The mandible is very pachyostotic, with a low anterior part. The transversal section of the anterior portion of the hemimandible is circular. Antlers terminate with a palmation. The proximal part of the antler beam has a circular transversal section and lacks basal tines. The tine inserted on the anterior side of the beam (homologous with the middle tine in *Megaloceros giganteus*) is situated from the burr at a distance ca. two times exceeding the diameter of the antler base.

Description. The cranial morphology of *M. algericus* is atypical and has no analogues among Cervidae. The skull is very broad, while the length proportions of the cranium are modified insignificantly; the skull breadth attains more than 60% of the condylobasal length (Fig. A.40). Splanchnocranium is relatively short: the length measured from the anterior edge of orbits to prosthion makes is shorter than 1/2 of condylobasal length. The position of *bregma* between the posterior edges of pedicles and the position of *nasion* slightly caudally to the anterior edges of eye sockets are similar to the morphological condition found in *M. giganteus*. The cranial bones are very thick, reminding the cranial hyperostosis described in *Megaloceros*. However, unlike in *Megaloceros*, the vomer is not affected by hyperossification. The zygomatic arches are markedly thin and feeble, contrasting with the overall robustness of the skull. The braincase is moderately flexed: the angle between parietal bones and face profile amounts to ca. 135° and shows an intermediate condition between *Dama* and *Megaloceros*. The parietal bones are flat. The pedicles are rather long, set obliquely on the skull and somewhat deflected toward the rear and the sides. The pedicles are slightly compressed in the anteroposterior direction, however, this compression is not as strong as in the advanced species of *Praemegaceros* (*P. verticornis*, *P. dawkinsi*, and *P. solilhacus*). The frontal bones are very broad (corresponding to the disproportionally broad skull), flat and slightly depressed from both sides of the frontal suture. The ethmoidal orifices are completely closed. The preorbital fossae are not developed. The nasal bones are relatively narrow and rather long, extending behind the imaginary line connecting the anterior edges of orbits, as in *Megaloceros* and *Dama dama* (but not as in *Dama clactoniana*). The orbitofrontal portion of the cranium is rather short, as in *Dama* and *Megaloceros*: the anterior edge of the orbit is situated above the M^2-M^3 border. The eye sockets are relatively large, as in *Dama*. The basioccipital is broad and bell-shaped. The *bullae tympani* are rather large, rounded, projecting outside (as in *Dama*), and compressed in the mediolateral direction. The anterior bony thorn of *bullae tympani* is not present in *Megaceroides*, unlike some Cervinae (*Cervus, Rucervus*). The relative length of the upper tooth row to the basal length of the skull amounts to 29.5%, being fairly close to the ratio found in *Megaloceros*, *Axis* and *Dama*. Nonetheless, the displacement toward the anterior position of the upper cheek tooth row represents a specific character of *M. algericus*. The diastemal part of the mandible is very short. The anterior portion of the mandible from M_1 to symphysis has a cylindrical shape. Behind M_1, the mandible became higher and more robust. The lower tooth row is displaced orally due to the very short diastema and obliquely set ascending portion of the mandible. The mandibular pachyostosis appears very early during ontogenetic development and is recorded even in juvenile individuals with deciduous teeth, although the juvenile mandible is less thick than the mature specimens.

Upper canines are absent. Cheek teeth are relatively small. The lower fourth premolar (P_4) is molarized: its metaconid is fused with the paraconid. The premolar series is comparatively short, however, a broad variation is observed here. The premolar/molar length ratio amounts to 60.5% in the mandible FIL166, while the same tooth series ratio in the two specimens from Phacocheres amounts to 45.0% and 52.9% (Hadjouis 1990). The lingual side of P^4 is not split into protocone and hypocone, not even grooved. The relative size of the upper third molar is visibly reduced; therefore M^2 is noticeably larger than M^3. The angle between labial and lingual walls of upper molars amounts to 37°, as in *Dama dama*. The hypoconal fold is present only in M^3. Two small enamel folds are found on the external side of the anterior hypoconal wing in M^2. Unlike the holotype of *M. algericus* from Hammam Meskoutin, the additional material discovered by Arambourg (1932, 1938) represents a deer with somewhat smaller upper cheek teeth (length of M^1-M^3 tooth series amounts to 54.1 mm in the specimen from Guyotville against 58.5 mm in the holotype of *M. algericus*). The cingulum in upper molars seems to be a variable character: it is well-developed in the type specimen from Hammam Meskoutin and is not developed in Arambourg's specimen. It is necessary to mention, that the type from Hammam Meskoutin does not show the specific size reduction of M^3. Possibly, the observed morphological differences may have a taxonomical significance at the species or subspecies level, but the available data are insufficient. However, if this is the case, one can distinguish two chronological forms of the endemic North African deer: an older larger form from Hammam Meskoutin with strong cingulum and normally developed M^3, and a more specialized descent form with smaller dentition, reduced cingulum and marked reduction of M^3. If this is true, the subspecies name Megaceroides algericus pachygenis (Pomel, 1892) should be applied to the form with pachyostotic mandibles and upper molars without a cingulum. In this case, the lower mandible, the isolated upper molar, the radius, and fragments of antlers from Berrouaghia (Algeria) figured by Pomel (1892: pl. VII-VIII) should be regarded as syntypes.

The complete antlers of *Megaceroides algericus* are unknown. The available material shows that the antlers are normally developed and do not show any sign of "degeneration" reported by Azzaroli (1979). Antlers are terminated with a palmation. The proximal part of the antler beam has a circular transversal section and lacks basal tines. The tine inserted on the anterior side of the beam (homologous with the middle tine in *Megaloceros giganteus*) is situated from the burr at a distance ca. two times exceeding the diameter of the antler base (Hadjouis, 1990; Croitor, 2016).

Unlike *Praemegaceros*, *Megaceroides* is characterized by the relatively longer braincase (a primitive character), the cylinder-shaped pedicles (not compressed anteroposteriorly or dorsoventrally as in some advanced species of *Praemegaceros*), the cranial and mandibular pachyostosis, and the long nasal bones (Croitor, 2006a, 2016). *Megaceroides* shares with *Dama* the broad bell-shaped basioccipital, the large orbits, the large rounded *bullae tympani*, the flexed braincase, the missing upper canines, and the similar proportions of the lower tooth row. However, the shape and relative length of the braincase, the position of the antler pedicles, the developed cingula in upper molars, and the cranial hyperostosis of *M. algericus* suggest its greater affinity with *M. giganteus* (Lydekker, 1890; Joleaud, 1914, 1916).

Distribution: Late Pleistocene – Holocene, northwestern Africa (ca. 24,000 to 6641-6009 yr. BP; Fernandez et al., 2015).

Genus *Dama* Frisch, 1775

Synonymy:

Notomegaceros Gliozzi and Malatesta, 1982

Nomenclatural acts. Gliozzi and Malatesta, (1982) created a subgenus *Praemegaceros* (*Notomegaceros*) for the endemic deer *C. elaphus carburangelensis* from the Pleistocene of Sicily. Abbazzi et al. (2001) recognized the close affinity of the Sicilian endemic deer with modern fallow deer. Thus, *Notomegaceros* Gliozzi and Malatesta, 1982 should be regarded as a junior synonym of *Dama*.

Azzaroli (1947) identified two forms of small deer in the Early Pleistocene deposits of Upper Valdarno, which he named *Dama nestii nestii* and *Dama nestii eurygonos*, based on their antlers. *Dama nestii nestii* had four-pointed antlers with a frontal orientation of the distal fork, while *Dama nestii eurygonos* had slightly more robust four-pointed antlers with a parasagittal orientation of the distal fork. Further discussions on the systematic position of small-sized deer from Upper Valdarno include the "*Dama*-like" (or "*Axis*-like") cervid forms from the Pliocene and Early Pleistocene of Europe. Among these cervid forms are deer with three-pointed antlers, such as *Cervus pardinensis* Croizet et Jobert, 1824, which were discovered in the Early Pliocene in Eastern Europe and the Late Pliocene in Western Europe. In the Early Pleistocene fauna of Western Europe, remains of another small cervid were found and described under various species, including *Cervus rhenanus* Dubois, 1904, *Cervus philisi* Schaub, 1941, *Cervus perolensis* Azzaroli, 1952, and *Cervus ichnoceros* Boeuf, Geraads, and Guth, 1992.

The systematic position of these "*Axis*-like" cervids remained unclear for several decades, and they were included in the arbitrary group "*Cervus sensu lato*" (Heintz, 1970), which reflects their uncertain phylogenetic and systematic relationship with the modern genus *Cervus*. De Lumley et al. (1988) also adopted a cautious approach and described *Cervus* (*sensu lato*) *nestii vallonnetensis* from the Latest Villafranchian of the Vallonnet Grotto (Southern France).

In 1992, Azzaroli created the genus *Pseudodama* as a taxonomical solution for the small-sized deer from the Pliocene and the Early Pleistocene of Western Europe. *Dama nestii* (= *Dama nestii nestii*) is the type species of *Pseudodama*, and other species included in the genus are *C. pardinensis*, *C. rhenanus*, *C. perolensis*, *Pseudodama lyra* Azzaroli, 1992, and *P. farnetensis* Azzaroli, 1992. The specimens previously described by Azzaroli (1947) as *Dama nestii eurygonos* were reported by Azzaroli (1992) as an advanced form of *Pseudodama nestii*. The comparative study of cranial and antler morphology demonstrated that *Pseudodama* with the genotype *Dama nestii nestii* is a junior synonym of *Cervus* Linnaeus (Croitor, 2006a). Only two "*Dama*-like" forms, *Dama nestii eurygonos* and *Pseudodama farnetensis*, actually belong to the genus *Dama*.

Diagnosis: medium to small-sized deer with a strongly flexed and relatively long braincase. The distance between the inion and bregma is always greater than the breadth of the braincase. The basioccipitale is broadened at the pharyngeal puberosities and has a bell-shaped appearance. The pedicles are short and vertical. The parietal bones are convex, and the orbits are relatively large. The upper canines are absent, and the lower fourth premolar is molarized. The angle of the basal tine ramification is always obtuse.

Composition: *D. eurygonos* Azzaroli, 1947 (Early Pleistocene, Italy); *D. vallonnetensis* (de Lumley, Kahlke, Moigne and Moulle, 1988) (late Early Pleistocene, Europe); *D. clactoniana* Falconer, 1868 (Middle Pleistocene, Western Europe); *D. 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.

Dama eurygonos Azzaroli, 1947

Synonymy:

1947 *Dama nestii eurygonos* ssp. nov.: Azzaroli, p. 56, fig. 5 (1).
1986 "*Dama*" *cf. nestii* (Azzaroli): De Giuli, p. 20, pl. 8-13.
1992 *Pseudodama nestii* (Azzaroli): Azzaroli, p. 16, fig. 5.
1992 *Pseudodama farnetensis* sp. nov.: Azzaroli, p. 19, fig. 10, Pl. 5, fig. 2, a-b.
1998 *Euraxis eurygonos* (Azzaroli): Di Stefano & Petronio, p. 53.
2001 *Dama eurygonos* (Azzaroli): Croitor, p. 98.
2003 *Axis eurygonos* (Azzaroli): Girotti et al., p. 88.

Nomenclatural acts. This small-sized cervid (estimated body mass of approximately 70-80 kg) from the Late Villafranchian of Upper Valdarno (Italy) was originally described by Azzaroli (1947) as *Dama nestii eurygonos*. It was distinguished from *D. nestii nestii* (which is regarded as *Cervus nestii* here) by its somewhat more robust antlers with an obtuse basal ramification and the parasagittal orientation of the distal fork. Azzaroli (1947) was the first to propose an evolutionary relationship between small deer from Upper Valdarno and living fallow deer. In 1992, Azzaroli interpreted *Dama nestii eurygonos* (the name *eurygonos* did not appear in Azzaroli's work) as an advanced form of *Dama nestii nestii* and placed them in the newly created genus *Pseudodama*. According to Azzaroli (1992), the close affinity of small Villafranchian deer with *Dama* had not been demonstrated. Croitor (2006b) elevated *Dama eurygonos* to the species level and suggested its close relationship with modern fallow deer. Pfeiffer (1999) and Petronio et al. (2013) regard the species under study as a primitive deer of the genus *Axis*. However, the bony labyrinth analysis carried out by Mennecart et al. (2017) confirmed the close phylogenetic relationship between *D. eurygonos* and modern *D. dama*.

Diagnosis: The species is somewhat larger than modern *D. dama*. The braincase is short, domed, and flexed. The orbitofrontal region of the skull is shortened, with the anterior edge of the orbit reaching the level of M^2. Orbits are relatively large, and pedicels are short and vertical on the skull roof. The frontal and parietal bones are convex. Unlike *D. dama*, the posterior edge of the nasal bones does not extend behind the line connecting the anterior edges of the eye sockets. The angle between the ascending and horizontal parts of mandible is 102°. The angle between the labial and lingual sides of the molars is comparatively oblique, at approximately 37°. P_4 is molarized. The antlers are robust, four-pointed, and widely spanned. The basal tine is situated at a little distance from the burr and forms an oblique angle with the antler beam. The distal fork is oriented in the parasagittal plane. The metapodial bones are long, and the metacarpus is longer than the radius or almost of the same length.

Holotype: the pair of antlers with pedicels and frontal bones IGF 245, MGUF.

Type locality: Tasso, Upper Valdarno (Central Italy).

Stratum typicum: the Late Villafranchian deposits of Upper Valdarno.

Description. The holotype of *D. eurygonos* is the antlered frontlet IGF245 (MGUF) of an adult male. Its frontal breadth is 105.5 mm (*D. dama*: 104.4 - 91.8 mm; n=9), while the breadth of the skull behind the pedicles is 89.5 mm (*D. dama*: 86.4 - 74.4 mm; n=9). The antlers are relatively robust and simple four-pointed, but the antler bauplan is typical for *Dama*: the first (basal) tine is strong and forms, with the antler beam, a very obtuse angle (ca. 120°) at a short distance from the burr. The distal fork is oriented in the parasagittal plane and is formed by a longer anterior tine that is a continuation of the beam and the posterior crown tine implanted on the posterior side of the beam. Although the antlers of modern fallow deer are palmated, the antler palmation in *D. dama* results from the fusion of multiple posterior tines. Therefore, the posterior insertion of crown tines is typical of the *Dama* antler bauplan (Fig. A.46, A). The second (middle) tine is relatively small in the type specimen and may be missing in younger individuals (Croitor, 2006b). The cross-section of the beam is circular. The beam segment between the basal and the middle tines and the beam segment between the middle tine and the distal fork are almost of equal length, so the second tine is in a more proximal position compared to *Cervus nestii*.

The damaged skull IGF 244 (MGUF) of *D. eurygonos* from Tasso already shows the typical *Dama* morphology: the flexed, short, and domed braincase, the convex frontal and parietal bones, the short pedicles in the vertical position, the relatively large orbits, the short orbitofrontal portion of the skull (the anterior edge of the orbit reaches the level of M^2), and the large ethmoidal openings. Unlike modern *D. dama*, the posterior edge of the nasal bones does not reach behind the line connecting the anterior edges of the eye sockets. The preorbital fossae are large and deep with sharply outlined edges. P_4 seems to be always molarized. Upper molars are more short-crowned compared to C. nestii: the angle between the lingual and labial walls of M^2 amounts to 37°.

Distribution. *D. eurygonos* inhabited the Italian Peninsula and Southeastern Europe during the Early Pleistocene (Late Villafranchian). It was absent in the Olivola F. U. and its first recorded appearance on the Italian peninsula was in the Tasso F. U. Additionally, a proximal part of an antler (Nr. 26/20 IZC) similar to that of *D. eurygonos* was discovered in Villafranchian deposits in Slobozia Mare, South Moldova (Croitor, 2006b)

Dama vallonnetensis (de Lumley, Kahlke, Moigne and Moulle, 1988)

Synonymy:

1963 *Cervus philisi* Schaub, 1941: de Lumley et al., p. 11, Fig. 2).

1977 *Cervus* (*Rusa*) *moldavicus* Janovskaya, 1954: Alekseeva, p. 129, Pl. XIX.

1979 *Dama nestii eurygonos* Azzaroli: Petronio, p.107, Fig. 2.

1988 “*Cervus*” (*s. l.*) *nestii vallonnetensis* n. ssp.: de Lumley *et a*l., p. 483, Fig. 14.

1998 *Pseudodama nestii vallonnetensis* (Kahlke) : Moullé, p. 34, Fig. 2.

2001 *Dama vallonnetensis* (de Lumley et al.) : Croitor, p. 99.

Diagnosis. The species is slightly larger than *D. dama*, and its antlers are long and robust with three points. The first bifurcation has a very oblique angle, and the first tine is strong, robust, and rests on the burr. The second (middle, trez) tine is reduced, while two long tines oriented in the parasagittal plane form the terminal fork. The anterior distal tine is a continuation of the beam, while the posterior distal tine springs off from the posterior side of the beam. The pedicels are short and vertically positioned. The braincase is domed and strongly flexed, the splanchnocranium is with large eye sockets and a short orbitofrontal part.

Holotype: a basal fragment of the left (not right, as indicated in the original description) shed antler Nr. 10170, MPRM (De Lumley et al., 1988: p. 179, fig. 14).

Locus typicus: Vallonnet (Roquebrune-Cap-Martin, Alpes Maritimes, France).

Stratum typicum. the Early Pleistocene deposits of the Vallonnet Cave.

Description. The body size of this species is intermediate between *D. dama* and *D. clactoniana*. The type specimen, a basal fragment of the left shed antler Nr. 10170, MPRM, is characterized by a very strong and massive basal tine situated very close to the burr, forming a very obtuse angle with the antler beam. The antler beam is set obliquely to the burr and is directed backward and sideways. The position of the basal tine distinguishes *D. vallonnetensis* from *D. eurygonos*, which has the tine mounted at a certain distance from the burr.

The sample from Vallonnet comprises mainly isolated teeth, mandible fragments, and several antler fragments. Some dental remains can be confidently ascribed to *D. vallonnetensis*. M^3 Nr. 1174 (RMPM) has a moderately oblique lingual wall that forms an angle of 37° with the labial wall of the tooth, as in *D. eurygonos*. The additional enamel folds and cingulum are absent. The fragment of the left hemimandible Nr. 7879 (RMPM) has a molarized P_4 and a relatively long premolar series (61.9% of the molar series length; L P_2-P_3 = 94.5 mm; L P_2-P_4 = 36.3 mm; L M_1-M_3 = 58.6 mm), which approaches the upper limits of relative premolar length in modern *D. dama* (46.0-61.6%).

The articulated skeleton of an adult *D. vallonnetensis* with antlers was reported by Petronio (1979) from the terminal Villafranchian of Capena (Italy). This specimen, initially identified by Petronio (1979) as *Dama nestii eurygonos*, exhibits specific morphological details in the distal portion of the antler. The antlers from Capena are characterized by a strong basal tine situated very close to the burr and a distal massive fork with the posterior insertion of the second crown tine, as in *D. eurygonos*. However, the middle tine is missing in the specimen from Capena, and the antlers represent a simplified three-pointed type of antler construction. Unlike *D. eurygonos*, the missing middle tine in *D. vallonnetensis* is a constant characteristic and not an early ontogenetic stage of antler development (Croitor, 2006b). Fallow deer with such a simplified antler shape are also known from Untermassfeld, Germany (Kahlke, 1997, 2001), and Etulia, Moldova (Alekseeva, 1977: tab. XIX). Alekseeva (1977) reported the antlers with skull fragments from Etulia as *Cervus* (*Rusa*) *moldavicus*, but the short and robust pedicles, convex parietal bones, and the three-pointed antlers with the low insertion of the first tine and the posterior insertion of the third tine on the beam are diagnostic characters of *D. vallonnetensis*

A slightly smaller form of *D. vallonnetensis* has been discovered in the final Villafranchian / Epivillafranchian of Pirro Nord (Italy). Articulated skeletons and complete antlered skulls have been recovered from this site. The cranial material from Pirro Nord confirms the close relationship between the Villafranchian fallow deer and *D. dama*, as evidenced by several shared features such as large and inflated bullae tympani, a flexed neurocranium, a broad contact of ethmoidal openings with nasale, and the absence of upper canines. The fallow deer from Pirro Nord is characterized by advanced molarization of P_4 and a relatively short premolar series (premolar/molar ratio ranging from 55.3% to 57.7%, n=3). In contrast to *D. dama*, the Pirro Nord fallow deer has shorter nasal bones that do not extend beyond the line connecting the anterior edges of orbits, a longer contact between the nasal and premaxillary bones, and comparatively broad and massive premaxillary bones that reflect adaptation to arid environmental conditions. The antlers of the Pirro Nord fallow deer are characterized by an obtuse first ramification situated very close to the burr, a vestigial posterior crown tine represented only by a small knob, and a missing middle tine. The described individual of fallow deer from Pirro Nord is a young adult male, very similar to *Dama vallonnetensis* (De Lumley et al., 1988) from Capena and Vallonnet.

Distribution. Latest Villafranchian – Postvillafranchian; Southern France, Spain, Italy, Germany, Greece.

Dama clactoniana Falconer, 1868

Synonymy:

1827 *Cervus* (*Dama*) *paleodama* Cuvier, 1823: Cuvier, p. 307.
1827 *Cervus* (*Dama*) *somonensis* Cuvier, 1823: Cuvier, p. 307.
1875 *Cervus euryceros* (Aldrovandi): Gastaldi, p. 440, fig. 1.
1892 *Cervus* (*Dama*) *Gastaldii* [sp. nov.]: Pohlig, p. 230, fig. 17.
2013 *Dama roberti* sp. nov.: Breda and Lister, p. 157, figs. 2-8.

Diagnosis. The body size is similar to that of modern Western European *Cervus elaphus*. The splanchnocranium is relatively longer compared to other species of *Dama*; the nasopremaxillary contact is elongated. The nasal bones are short and do not extend beyond the level of the anterior orbital edges. The anterior edge of orbit is situated above M^2. Antlers are distinguished by a well-developed distal palmation, the strong development of a middle tine, and the presence of an anterior crown tine.

Description. This is the largest species within the genus (weighing approximately 140 kg) found in the Middle Pleistocene of Western Europe, and the first fallow deer species with palmated antlers. The antlers of *D. clactoniana* are distinguished by multiple crown tines inserted on both the anterior and posterior sides of the palmation axe, in contrast to modern *D. dama* (Leonardi and Petronio, 1976). While this deer species has a relatively long face, its face lengthening differs from that of *C. elaphus*. The anterior edge of the orbits in *D. clactoniana*, as observed in specimen "Riano 6" (MPS), is situated above M^2, indicating that the orbitofrontal part of the skull is not elongated. A partially preserved skull from Swanscombe (Sw-71, NHML) shows a similar facial morphology to the fallow deer from Pirro Nord, where the nasal bones hardly reach the anterior orbital line and the articulation between the nasal and premaxillary bones is much longer than in *D. dama*.

Pohlig (1892) described a new species, *Cervus* (*Dama*) *gastaldi*, based on an antler from the upper part of the Po Valley that was originally reported and illustrated by Gastaldi (1875). *Dama roberti*, another Middle Pleistocene species of fallow deer, was recently described by Breda and Lister (2013) from Pakefield (England) and Soleilhac (France). The antlers are characterized by a typical *Dama* obtuse basal ramification and a strong curved basal tine. The antler beam is straight with a narrow flattened expansion in its distal part. Breda and Lister (2013) suggest that the specimen from Pakefield represents an adult individual; however, its vertically set pedicles (a typical character of *Dama*) are relatively too long, indicating a young age. The articulations between cranial bones (Breda and Lister, 2013: p. 159, fig. 3) are not obliterated, confirming the young individual's age. Therefore, it is highly probable that the unusually simple antlers from Pakefield and Soleilhac represent just an early ontogenetic stage of development. This view may be confirmed by the young specimen No. 19 B.M. of *Dama clactoniana* from Swanscombe (Leonardi and Petronio, 1976: p. 22, fig. 28), which is also characterized by the presence of only one basal tine and a distal narrow blade-like extension. Earlier, we identified the antler of the fallow deer from Soleilhac as a juvenile specimen of *Dama clactoniana* (Croitor et al., 2006), and we do not see any convincing arguments that may change our opinion

Dama dama (Linnaeus, 1758)

Diagnosis: Small to medium-sized deer with complex palmate antlers bearing thin, curved basal tines located a short distance from the burr and well-developed middle tines. The antler palmation is formed by fused posterior crown tines in the distal portion, while anterior crown tines are absent. Nasal bones are long, extending behind the imaginary line connecting the anterior edges of orbits, and the contact between premaxillary and nasal bones is very short.

Description. Di Stefano and Petronio (1997) reported the earliest known modern-type fallow deer, *D. dama tiberina*, from the late Middle Pleistocene of the middle Aurelian mammal age. This new chronosubspecies can be distinguished from *D. clactoniana* by its smaller body size and less exaggerated antlers, which lack anterior crown tines. *D. dama tiberina* also has a narrower palmation and fewer posterior crown tines compared to *D. dama dama* (Di Stefano and Petronio, 1997). Abbazzi et al. (2001) suggested a close relationship between *D. dama tiberina* and *Megaloceros calabriae* Bonfiglio, 1978, from Bovetto, Southern Calabria, and referred to the deer from Bovetto as *D. dama* cf. *tiberina*. If the synonymy of these subspecies is confirmed, the oldest modern fallow deer subspecies should be named *D. dama calabriae* (Bonfiglio, 1978) accorfing to the principle of priority, and if not, the name *D. dama calabriae* will remain restricted to the sample from Bovetto.

D. dama geiselana is a large subspecies of fallow deer found in Northwestern Europe, comparable in size to *D. clactoniana*. Its antlers terminate in a strong palmation that often is supplemented with more or less detached lowermost crown tine. The basal tine is cylinder-shaped and robust, and some variants of antler morphology have a flattened proximal beam and supplementary small prongs between the basal and middle tines, reminiscent of *Dama mesopotamica*. P_4 is variable and, in some cases, not fully molarized. *D. dama geiselana* can be differentiated from *D. clactoniana* by the shape of the palmation and the absence of anterior crown tines (Pfeiffer, 1998).

Distribution: Late Pleistocene – Holocene; Mediterranean Europe – Anatolia.

Dama carburangelensis (De Gregorio, 1925)

Synonymy:

1925 *Cervus elaphus carburangelensis* [ssp. nov.]: De Gregorio, p. 8, pls. XVIII-XX.

1982 *Praemegaceros* (*Notomegaceros*) *carburangelensis* (De Gregorio, 1925): Gliozzi and Malatesta, p. 315.

1990 *Megaceros* (*Notomegaceros*) *carburangelensis* (De Gregorio, 1925): Petronio, p. 261.

2000 *Megaceros carburangelensis* (De Gregorio, 1925): Pereira, p. 205.

2001 *Dama carburangelensis* (De Gregorio, 1925): Abbazzi et al., p. 31.

Nomenclatural acts. The small-sized deer from the Pleistocene of Sicily was originally described as an endemic subspecies of red deer by De Gregorio in 1925. Later, following the systematic model proposed by Azzaroli (1961), the Sicilian deer was reclassified as a dwarfed giant deer of the "*verticornis* group" and placed in its own subgenus *Notomegaceros* within the genera *Praemegaceros* or *Megaceros* (Gliozzi and Malatesta, 1982; Vislobokova, 1990; Petronio, 1990). Abbazzi et al. (2001) further reclassified De Gregorio's deer from Sicily as *Dama carburangelensis* based on cranial and antler morphology.

Emended diagnosis: the body size of this species is slightly smaller than that of modern fallow deer. The basal tine of the antlers is robust, short, and positioned very close to the burr. The middle tine is well-developed, and the posterior tine is directed laterally and posteriorly, located distally at a short distance from the middle tine. The antlers terminate in a narrow palmation formed by coalesced posterior crown tines. The anterior crown tines absent.

Description. The estimated body mass is approximately 62 kg. According to Gliozzi and Malatesta (1982), the cranial morphology of *Dama carburangelensis* is typical of the *Dama genus*. The antlers of this species feature a strong basal tine, a well-developed middle tine, and a small but noticeable palmation with three posterior crown tines. An accessory tine is located above the middle tine on the posterolateral side of the beam, which could be an accidental accessory prong or an example of convergent evolution in cervids adapted to open landscapes (such as *Megaloceros giganteus*, *Praemegaceros verticornis*, and *Rangifer tarandus*). The premolar/molar ratio mean value (60.4%) reported by Gliozzi and Malatesta (1982) indicates a relatively longer premolar series compared to continental fallow deer. This characteristic is reminiscent of another

Mediterranean insular deer, *Praemegaceros cazioti*, which also evolved a longer cheek tooth row due to premolar series elongation.

Distribution: an insular endemic of the post-Tyrrenian age (late Middle Pleistocene – Late Pleistocene), Sicily.

Cervinae incertae sedis

“*Cervus*” *australis* de Serres, 1838

The systematic position of this plesiometacarpal deer, which is similar in size to *Capreolus*, is not yet fully resolved. The species is based on a small shed antler with a single bifurcation positioned very high, found in the Early Pliocene of Montpellier, France (de Serres 1838). Unfortunately, there is no additional material from the type locality. Depéret (1890) suggested that *Cervus* (*Capreolus*) *ruscinensis*, based on a fine antlered skull with spike-like antlers, could represent a young individual of "*Cervus*” *australis* (which Depéret considered to be *Capreolus australis*). Despite the assumed young age of the type specimen of *Cervus* (*Capreolus*) *ruscinensis*, it is characterized by very short and divergent pedicles. Korotkevich (1970) and Vislobokova (1990) included “*Cervus*” *australis* in the genus *Paracervulus*. However, it is worth noting that the antler with a pedicle from Kuchurgan described by Korotkevich (1970) as "*Paracervulus australis*” has a relatively long pedicle. Teilhard de Chardin and Trassaert (1937) created the genus Paracervulus for quite large cervids with simple antlers, characterized by a high-situated bifurcation. It is possible that some of the specimens described by Teilhard de Chardin and Trassaert (1937: fig. 4, *Paracervulus bidens*) belong to *Procapreolus*. Simpson (1945) regarded *Paracervulus* as a junior synonym of *Metacervulus* Teilhard de Chardin and Trassaert, 1937. Asian *Metacervulus* is distinguished from “*Cervus*” *australis* and “*Cervus*” *ruscinensis* by its flattened antlers. Therefore, the systematic position of “*Cervus*” *australis* and “*Cervus*” *ruscinensis* remains unresolved.

4.2. Conclusions to Chapter 4

1) The taxonomic diversity of plesiometacarpal deer in the Plio-Pleistocene western Palearctic region is represented by at least 16 genera, including two endemic genera found on Mediterranean islands (Croitor, 2018b).

2) The earliest members of the subfamily Cervinae dispersed into western Eurasia during the Early Pliocene. Unlike their Arian counterparts, they exhibited varying degrees of evolutionary specialization (Croitor and Stefaniak, 2009; Croitor, 2017).

3) Representatives of the subfamily Cervinae rapidly achieved a high level of taxonomic and eco-morphological diversity in the Western Palearctic during the Late Pliocene and Pleistocene. The taxonomic diversity of Cervinae reached its zenith during the Early and Middle Pleistocene (Croitor, 2018b).

4) In contrast to Capreolinae, Cervinae in the western Palearctic demonstrated greater evolutionary plasticity and repeatedly colonized islands, where they evolved into endemic dwarfed forms (Croitor et al., 2006).

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 found in advanced cervids represent a specific adaptation that "softens" sexual selection and diminishes excessive male mortality during intraspecific combats. The most proximal antler tine, the brow tine, appears very early in cervid evolution and serves the locally restricted purpose of protecting the eyes and face during combats (Lister, 1987). The second proximal tine, the bez tine, is specific only to *C. elaphus* and *C. canadensis* and appeared in the evolution of *Cervus* during the early Middle Pleistocene, coinciding with a significant increase in body size. The estimated body mass of 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*, reached approximately 237 kg (estimated based on occipital height; the sample includes cranial material from the Tiraspolian gravel and specimens studied by Di Stefano and Petronio, 1992; sample size = 14). Thus, a fourfold increase in body size is observed in the *C. nestii – C. elaphus acoronatus* lineage during the Early Pleistocene–early Middle Pleistocene transition.

Petrie (1988) suggested that larger animals may have greater capacities to injure each other during intraspecific contests, which could explain why red deer (and wapiti too, apparently) acquired the second basal tine, enhancing face protection during combats. It is interesting to note that the bez tine has a trend of diminishing in European red deer during the Late Pleistocene and Holocene, coinciding with body size reduction (Lister, 1987). However, the direct relationship between body size and the strength of the bez tine in red deer cannot be considered proven, as the bez tine is quite weak in the largest modern red deer subspecies, *C. elaphus maral* (Heptner and Zalkin, 1947; Flerov, 1952). Lister (1987) suggested 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.

The trez (or middle) tine appears early in the evolution of the subfamily Cervinae as a second ramification and coincides with the increase in body size and reduction of upper canines, making male antlers the only dangerous weapon against conspecific rivals (Geist, 1971). The development of this tine must have increased the safety of combatting stags that reached a certain body mass threshold, increasing the risk of lethal wounding. Kitchener (1987) suggested that the trez tine has a protective function against a rival's antlers, especially in cervids that bear complicated antlers, such as red deer and giant deer. The importance of additional antler tines in red deer stags was demonstrated by Davitashvili (1961) using examples of old bucks with degenerated and simplified antlers, which can easily wound and kill their conspecific rivals.

A forwardly pointed tine located in the middle of the antler beam appeared several times independently in the evolution of cervines. This is the case of the middle tine of *Praemegaceros verticornis* from the Middle Pleistocene of Europe, which appeared quite late in the *Praemegaceros* lineage, as it is completely absent in *P. pliotarandoides* from the late Early Pleistocene (Croitor, 2006b). The middle tine of *P. verticornis* is analogous to the trez tine of *C. elaphus* and *C. canadensis* and probably had the same function of locking the rival's antlers, but 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 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 evolve in cervids from middle latitudes and are not present in southern lineages with large antlers, such as Rucervus and Panolia. One possible explanation is that male survival is subjected to greater pressure in cervids from temperate latitudes with cold winters and a seasonal drop in forage. The pressure of seasonal male mortality, particularly among young and prime-adult stags, is significant (Clutton-Brock et al., 1982). As a result, additional security adaptations in antler shape help reduce excessive male losses during combat and compensate for seasonal male mortality. Therefore, a direct relationship can be assumed between harsh environmental conditions with a seasonal drop in temperatures and forage availability and the development of richly branched antlers. 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.

The posterior tine is an important feature of antlers in cervids that inhabit open landscapes. Typically, this tine is situated on the back side of the beam and below the crown part of the antler. It appears independently in several cervid lineages of the Cervinae and Capreolinae subfamilies, including the genera *Rangifer*, *Megaloceros*, *Praemegaceros*, *Praedama*, *Sinomegaceros*, and some species of the genus *Dama*. The lowermost posterior crown tine in *Dama geiselana* and *D. clactoniana* is typically very large, strong, and detached from the palmation (Leonardi and Petronio, 1976; Pfeiffer, 1998).

The occurrence of a posterior tine and its analogues does not depend on body size (it is developed in the giant continental *Praemegaceros* and *Megaloceros*, in some small-sized insular dwarfs, and medium-sized *Rangifer*) and is not correlated with the development of palmations or other parts of antlers. The stability of the development of posterior tine within the individual variation range (for instance, in the series of antlers of *Megaloceros giganteus* figured by Reynolds, 1929) suggests an important evolutionary selection in the favour of this character, which appeared repeatedly and independently in several lineages of the family Cervidae. Therefore, one can assume a certain biological importance of this part of antlers.

The adaptation to more or less open environments is the only circumstance that unites the deer with posterior antler tine. The most plausible explanation of the iterative development of the posterior tine during the evolution of cervids is its specific function of the defence against ectoparasites in rutting males. The study of rutting males of North American deer and territorial African antelopes revealed that the involvement of males in rutting decreases the behavioural and immune defence of males against ticks, which distract them from the rutting behaviour and bring damages to their physical and health state (Hart, 1997; Mooring et al., 2004). The priority of the investment into the rutting activity over the antiparasite defence has a negative consequence for males, which are exposed to a greater parasite load. Rutting impala males, for example, which self-oral groomed at one-third the rate of females, were found to carry about six times more adult ticks than females (Hart, 1997). Observations on male white-tailed deer reveal they had about 3 times as many adult ticks as females (Main et al., 1981). Mooring et al. (2004) suppose that the elevated testosterone level in rutting stags suppresses the grooming behaviour to increase male's vigilance, so the increased ectoparasite burden is a frequent side effect in rutting males. It is interesting to notice that the scratch grooming in males of the observed species was not affected by the rutting behaviour (Hart, 1997).

One can assume that the posterior tine in cervids is a specialized adaptation for scratch grooming in rutting males that eventually indirectly increase their combat capacities (Croitor, 2016). The evolutionary acquisition of the scratch grooming tine (the posterior tine) indirectly influenced mating success by diminishing the ectoparasite burden and improving the vigilance and physical state of the rutting stags. According to the available bibliographic data, the disturbing effect of ectoparasites during the rutting period may be important. The observations of modern North American wapiti revealed that September and October constitute the peak time for feeding by larvae of winter tick *Dermacentor albipictus* (Mooring and Samuel, 1998). This stage of the parasite biological cycle coincides with the rutting season in elaphine deer (Flerov, 1952; Sokolov, 1959) and therefore has an important negative influence over the physical state and the rutting success of stags. The use of antlers for scratch grooming is rarely reported for modern cervids, which are mostly adapted to wooded and ecotone habitats (Mooring et al., 2004), but it is recorded in *Rangifer tarandus tarandus*, the only modern deer adapted to open environments (Kynkäänniemi et al., 2014).

5.2. Multivariate analysis of craniodental characters and phylogenetic relationships

Capreolinae is distinguished from the subfamily Cervinae by its generally conservative *Capreolus*-like antler bauplan (Croitor, 2021), which is present in nearly all evolutionary lineages except for those with evolutionary simplification of antlers, such as *Mazama* and *Pudu*. The initial *Capreolus*-like antler bauplan is characterized by the first ramification being in a very high position, with the posterior branch bifurcating to form two tines of roughly equal size. This bauplan is found in *Procapreolus*, *Capreolus*, and *Eocoileus*, and was named the "forked type of antlers" by Lydekker (1898). Samejima and Matsuoka (2020) have shown that the morphological elements of the three-pointed antlers (the first tine and the distal fork) of *Cervinae* and *Capreolinae* are structurally different and not homologous. It appears that the evolutionary potential of the two distal ramifications is equal, as evidenced by the evolutionary specializations found within Capreolinae with stronger development of either the posterior branch (*Pliocervus*, *Pavlodaria*, *Alces*) or the anterior branch (*Capreolus*, *Procapreolus*, *Odocoileus*, *Rangifer*, *Neomegaloceros*). Although the conservatism in antler evolution was previously interpreted as a generally more primitive characteristic of Capreolinae compared to Cervinae (Czyżewska, 1968), it is now more appropriate to view it as two different ways of evolution and development of antlers within Cervidae (Samejima and Matsuoka, 2020). In practice, the diversity of telemetacarpal deer antlers is a combination of a limited number of variants of antler branch bifurcations (see Fig. 4.1).

The general antler bauplan and some details of antler morphology suggest the phylogenetic unity of the so-called “Pliocervines” from the Late Miocene of Europe and their close affinity with Capreolinae. All of them are characterized by the basic *Capreolus*-like antler bauplan, which may be recognized even in the quite specialized *M. variabilis* and modern *A. alces* (Fig. 1). Brooke (1878) has already defined the structure of antlers of Alces as dichotomous and noted the similarity of modern elk’s antler bauplan with *Blastocerus dichotomus*. In all the above-mentioned cases, one can distinguish the relatively high position of the first tine and the invariable distal parasagittal fork. This distal fork is well-distinguishable in *D. bessarabiae* and *M. variabilis*, and it terminates the palmation formed by the extension of the second beam segment. At fully-grown antlers of *D. bessarabiae*, the distal fork is supplemented with an accessory distal tine, while in *M. variabilis*, each tine of the distal fork is bifurcated or trifurcated (Fig. 4.1 C).

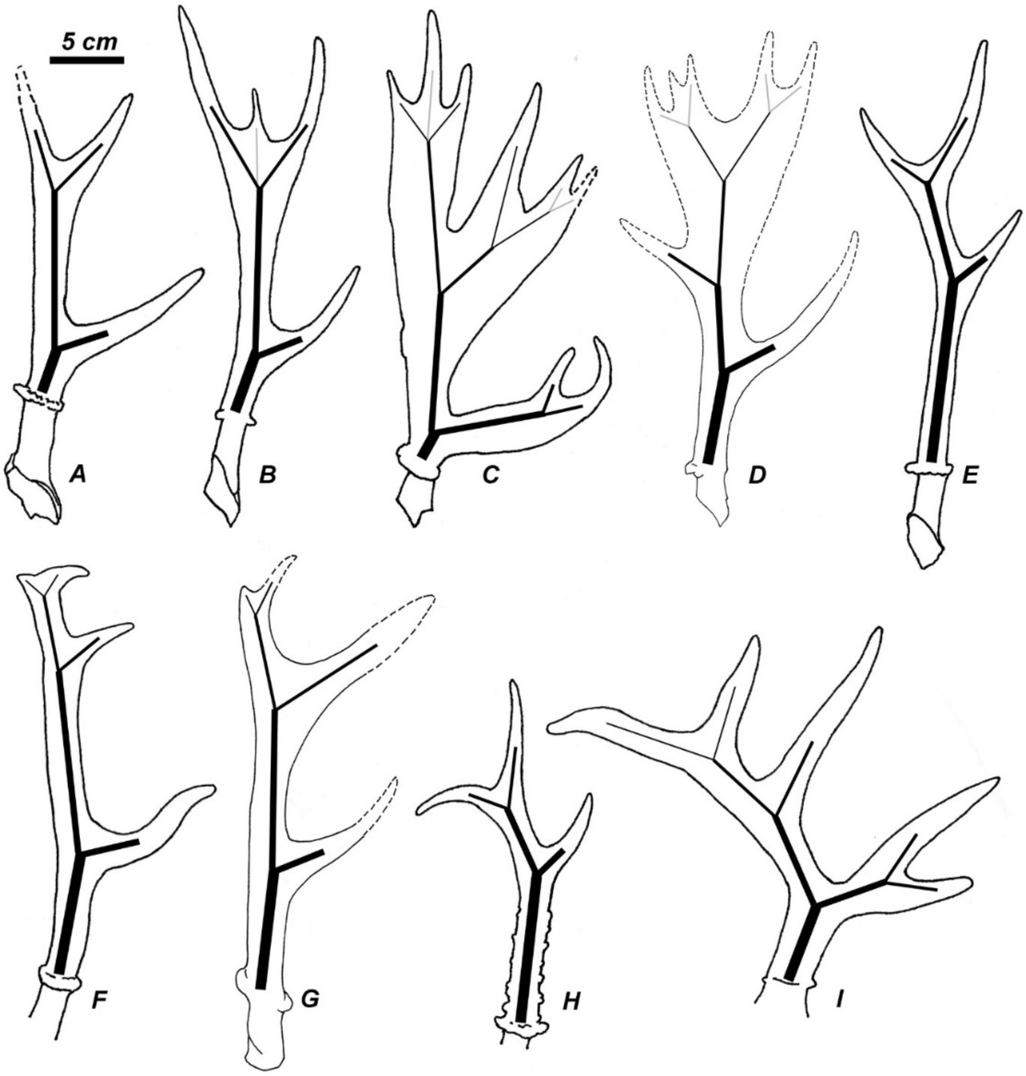

Fig. 4.1. The antler bauplan of Capreolinae: A, *Eocoileus gentriorum* from the Pliocene of North America (adapted from Webb 2000); B, *Damacerus bessarabiae* from the Late Miocene of Southeastern Europe (adapted from Khomenko 1913); C, *Metadicrocerus variabilis* from the Late Miocene of Southeastern 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 basic *Capreolus*-like antler structure is characteristic of the earliest New World cervid, *Eocoileus gentryorum* (Fig. 4.1 A). Antlers of *Odocoileus virginianus* generally maintain the initial *Capreolus* antler structure, but the distal part of the antler develops a crown. The first crown tine in *Odocoileus* is inserted on the posterior side of the beam (Pocock, 1912) and should be regarded as a homology of the posterior tine of the distal bifurcation in *Capreolus*. The subsequent crown ramifications represent metameric additions of new posterior crown tines. The anterior tine of the distal bifurcation in *Capreolus* is homologous with the main axis of the crown in *Odocoileus* that is curved forwards, downwards, and inwards (Brooke, 1878).

Rangifer tarandus developed the crown part of the antler composed of a series of posterior crown tines similar to that of *Odocoileus*. Some juvenile reindeer antlers variants exhibit the typical *Capreolus*-like structure (Croitor, 2021). As in *Odocoileus*, the largest proximal crown tine is homologous to the posterior tine of the distal bifurcation in *Capreolus*. The posterior tine inserted on the bowed part of the antler beam and the asymmetric basal “brow tine” represent later evolutionary acquisitions of reindeer.

The evolutionary lineage of elks (moose) displays an extremely broad variety of the basal portion length between the burr and the first ramification. The basal segment of the antler is shortened in Alces alces but is extremely elongated in *A. gallicus*. The basal portion of the antler in A. gallicus is transformed into an exceptionally long beam that extends into a small palmation on its distal extremity. As in all telemetacarpal deer, the small palmation of A. gallicus maintains the basic *Capreolus*-like bauplan. The hypothesized loss of basal tines in elks based on a few specimens with tines on the beam sounds doubtful. Aleksejeva (1980) figures two incomplete antlers with a tine on the antler beam that was interpreted as an atavistic basal tine; however, the antlers are incomplete, and the "atavistic" basal tines, which are situated quite high above the burr, may be the ordinary first ramification detached from the distal fork. Boeskorov (2006) regards those prongs on antler beams as "additional tines," and this viewpoint is accepted in the present study. One cannot exclude a spontaneous development of an additional basal tine in elks (Boeskorov, 2001: fig. 29-P), analogous to the "brow tine" in *Rangifer*. The questioned assumptions on an initial basal tine reduction in elks resulted in a confusing, complicated model of *Alces* antler evolution that does not permit tracing the homology with antlers of other Capreolinae (Samejima and Matsuoka, 2020). The four-pointed antlers of *Pliocervus* and *Pavlodaria* have developed from the subsequent bifurcation of the posterior branch of the initial distal bifurcation (Fig. 4.1 F, G).

Old World telemetacarpal deer. The multivariate analysis based on craniodental characters (including antlers) and some postcranial features places the extinct Old World genera *Metadicrocerus*, *Damacerus*, *Pliocervus*, *Procapreolus*, and *Lucentia* among the selected genera of modern capreolines. *Lucentia iberica* is a peculiar small-sized cervid from the Late Miocene of the Iberian Peninsula (MN11), characterized by simple two-pointed antlers with a high bifurcation position and a unique dental morphology (molarized P_4, upper molars supplemented with protoconal fold, lower molars with *Palaeomeryx* fold) (Azanza and Montoya, 1995). Azanza and Montoya (1995) noted the similarity of Lucentia's antlers with those of *Capreolus* and European

"Pliocervines" and suggested that the Iberian deer could represent an evolutionary stage preceding the dichotomy of cervines and capreolines, placing *Lucentia* closer to Cervinae. However, Azanza and Montoya (1995) regard the emerging protoconal fold in the upper molars of *L. iberica* as an important diagnostic apomorphy of the telemetacarpal deer. One can assume with some confidence that *L. iberica* represents the most primitive two-pointed stage of antler evolution of Capreolinae, although its dentition is already specialized and shows specific features of capreoline deer.

Possibly, the "Muntiacinae gen. et sp. indet." described by Azanza (2000) from the Early Turolian of Crevillente-2 (Alicante, Spain) represents a more primitive type of early capreoline evolutionary diversification. This cervid is characterized by a small size similar to modern muntjacs. However, its dental morphology is characterized by advanced characteristics, such as the emerging protoconal fold and labiolingually narrowed crowns of upper molars, which are correlated with the evolutionary trend towards mesosodont specialization (Croitor et al., 2020). The "muntiacine" from Crevillente-2, characterized by more advanced high-crowned upper molars with an emerging protoconal fold, represents an evolutionary specialization similar to the dental morphology of capreolines and possibly represents the early "muntjac-like" stage of Capreolinae evolution.

The results of the multivariate analysis suggest a cluster between *Lucentia iberica*, *Pliocervus matheroni*, and *Pavlodaria orlovi*, which may seem unexpected but is not contradictory. *Pliocervus* and *Pavlodaria* evolved a less common antler bauplan in *Capreolinae*, with further bifurcation of the posterior branch of the initial distal fork. Thus, 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 should be noted that the further bifurcation of the anterior or posterior branch of the initial distal bifurcation could often represent a parallelism in the evolution of Capreolinae and should not be considered a significant systematic character. *L. iberica* shares with *P. matheroni* the subtriangular cross-section of the distal portion of the antler, but the Iberian cervid cannot be regarded as a forerunner of *Pliocervus* since it already exhibits an advanced molarization of P_4.

Procapreolus is a relatively less specialized *Capreolinae* cervid with three-pointed antlers. While some of its features may superficially resemble muntiacines, such as the quite long pedicles, short nasal bones, large preorbital pits, and large upper canines, its basicranial morphology (Valli, 2010) and specialized cheek teeth (including the presence of the *Palaeomeryx* fold, strong protoconal fold in upper molars, and advanced molarization of P_4) place *Procapreolus* within Capreolinae. *Lucentia pierensis* (not included in the analysis) shows some morphological features of two-pointed antlers (such as the cylindrical antler axis and sub-rectangular antler cross-section in the area of ramification: Azanza and Montoya 1995: fig. 6) that approach it to *Procapreolus*. The genera *Damacerus* and *Metadicrocerus* are the closest to *Procapreolus* and share most of the primitive features combined with typical features of Capreolinae, including the *Capreolus*-like antler bauplan. *Turiacemas concudensis* from the Late Miocene of the Iberian Peninsula is possibly related to *Damacerus* and *Metadicrocerus*, based on the 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 cervid remains from Dytiko (Greece, MN13) described by Bouvrain and de Bonis (2007) as "? *Procapreolus* sp." are possibly related to *D. bessarabiae* but are certainly not conspecific. The Greek material is represented by fine dental remains and characterized by a specific combination of advanced and primitive characters: P_4 is not molarized, lower molars are supplemented with a *Palaeomeryx* fold, and upper molars have an additional protoconal fold and a hypoconal spur. Bouvrain and de Bonis (2007) suggested that the cervid from Dytiko was related to *Pavlodaria* and *Procapreolus*, but its exact systematic position remained unclear. The primitive P_4 rules out its attribution to *Procapreolus* and suggests it is more similar to *D. bessarabiae* and *P. matheroni*. However, unlike those two species, the deer from Dytiko is characterized by the more advanced shape of the upper molar crowns, which are narrower and represent an evolutionary advancement toward hypsodonty. The deer from Dytiko belongs to a new species, but a conclusive opinion is only possible when diagnostic characteristics of antler morphology are available.

The Late Miocene saw the emergence of several cervid genera with a *Capreolus*-like antler bauplan, including *Procapreolus*, *Damacerus*, and *Metadicrocerus*, and possibly *Turiacemas*. *Neomegaloceros gracilis* (Fig. 4.1 D) and *Palaeaxis loczyi*, also belong to this evolutionary radiation of telemetacarpal deer in Eastern Europe. *N. gracilis* is a relatively advanced deer with short and anteroposteriorly compressed pedicles and a high position of the first ramification. The study of the type specimen cast stored in MNHU revealed a partially destroyed distal antler portion with a bilobed palmation that was terminated by four or five distal tines, and a triangular cross-section of the first tine, similar to *Damacerus* and *Metadicrocerus*. *N. gracilis* has a well-developed posterior tine that may be a homology of the posterior tine in *Capreolus*-like antlers.

Although the genus *Alces* is related to the Late Miocene radiation of Capreolinae in Europe, the earliest occurrence of elks is reported from 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 (still present in *Alces gallicus*), the development of the protoconal fold in upper molars, the rectangular shape of beam cross-section below the palmation, and the development of additional antler prongs and tine bifurcations. However, *Damacerus* and *Metadicrocerus* cannot be regarded as probable forerunners of *Alces* because they are characterized by the advanced morphological trait of having nasal bones extending caudally to the imaginary line connecting the anterior edges of the orbits. The geographic center of elk evolution is most probably situated in the eastern regions of Eurasia, where the earliest remains of *Alces* have been found (Vislobokova et al., 1995).

Cervodama pontoborealis Pidoplichko and Flerov, 1952, from Mariupol is a specialized Capreolinae deer that belongs to the Late Miocene evolutionary radiation of telemetacarpal deer. Its palmated antlers superficially resemble those of modern *Alces* (Korotkevich, 1970; Vislobokova, 1990). However, the antler bauplan of *C. pontoborealis* is not identical to that of *A. alces*. Unlike modern elk antlers, the tines of the distal fork are stronger and do not form further dichotomous bifurcations.

A. gallicus has been considered the most primitive direct ancestor of modern elks, 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 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 a specialized side evolutionary 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. The same neurocranial index in *A. latifrons* from Mundesley (M6553, NHML) is 85.5%, indicating the primitive elongated proportion. The extremely elongated basal segment of antlers (between the burr and the first ramification) in *A. gallicus* is, therefore, a far-reaching evolutionary specialization of the side phylogenetic branch, not an initial primitive feature of elk antlers. Consequently, the provided data on relative braincase length does not support Boeskorov's (2005, 2006) view that *A. latifrons* is a giant descent of *A. gallicus*. Nonetheless, I agree with Boeskorov (2005) that *A. latifrons* could not be a direct ancestor of modern *A. alces* following the principle of 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). In my opinion, *T. caucasicus* from the final stage of the Early Pleistocene of the Taman Peninsula is a junior synonym of *Praemegaceros solilhacus* (Croitor, 2006a), while *P. mirandus* from the Pliocene of Kosiakino is a giraffid (Croitor, 2018a).

The multivariate analysis based on craniodental characteristics places *Capreolus* together with Hydropotes (Fig. 4.2), which is consistent with modern genetic studies (Randi et al., 1998; Gilbert et al., 2006). *C. capreolus* is distinguished by the relatively short distance between parallel pedicles, similar to *Pliocervus* and *Pavlodaria*. However, unlike *Pliocervus* and *Pavlodaria*, the pedicles of *Capreolus* are positioned vertically on the skull roof. The short distance and parallel orientation of pedicles in modern roe deer might be a secondary evolutionary acquisition, as the oldest species of the genus, *Capreolus constantini*, is characterized by moderately divergent pedicles, with a distance between them exceeding the pedicle diameter (Vislobokova et al., 1995; Ogino et al., 2009).

The results indicate that the antlerless deer *Hydropotes* inermis is closely associated with Capreolus. While the absence of antlers in *Hydropotes* has long been considered a primitive morphological condition (Flerov, 1952), it is actually a far-reaching evolutionary specialization. The origin of the remarkably specialized genus *Hydropotes* remains unclear from the paleontological record. However, *Platycemas infans* Teilhard de Chardin and Trassaert, 1937, from the Late Tertiary of Shansi (China), is characterized by very small antlers that appear secondarily reduced. The antler of *P. infans* is set on a normally developed burr but is significantly smaller in size, maintaining all the elements of a three-pointed *Capreolus*-like antler (Teilhard de Chardin and Trassaert, 1937: fig. 8). Dong and Ye (1997) suggested that the type specimen of *P.* infans is a pathological variation form of *Cervavitus novorossiae*. However, another discovery of a *Platycemas* antler from the Pliocene of Mongolia (Vislobokova, 1983) suggests that we are dealing with a true species with remarkably reduced antlers. Modern New World genera *Mazama* and *Pudu* also exhibit a similar secondary reduction of antlers among Capreolines. Understanding the origin and evolution of *P. infans* may provide insight into the origin of *H. inermis*.

Rangifer tarandus and *Rangifer* sp. from the Early Pleistocene of Isakovka-4, Siberia, are associated with *Odocoileus virginianus* (Fig. 4.2). The Early Pleistocene *Rangifer* shares with modern reindeer the shape of the neurocranium and dental morphology but retains the primitive, parallel, and the caudally inclined pedicles (Webb, 2000; Bondarev et al., 2017). *Rangifer* and *Odocoileus* both exhibit the complete division of the nasal cavity by a vertical plate of the vomer and a unique characteristic, the development of the crown part of the antler.

Small-sized representatives of the subfamily Cervinae. The taxonomy and systematic position of the so-called "*Dama*-like" or "*Axis*-like" small-sized deer from the Pliocene and Early Pleistocene of Europe have been a subject of contradictory opinions. This is mainly due to an inadequate and superficial assessment of the importance of certain antler and postcranial skeleton morphological features. To address this, a hierarchical cluster analysis was conducted using available diagnostic cranial, dental, and antler characteristics of the "*Dama*-like" deer and some well-known modern species, such as *Cervus elaphus*, *Axis axis*, *Dama dama*, *Rusa unicolor*, and *R. timorensis*. The analysis revealed a complicated systematic situation of the fossil small-sized deer, which cannot be classified under a single genus name *Pseudodama* (Fig. 4.3).

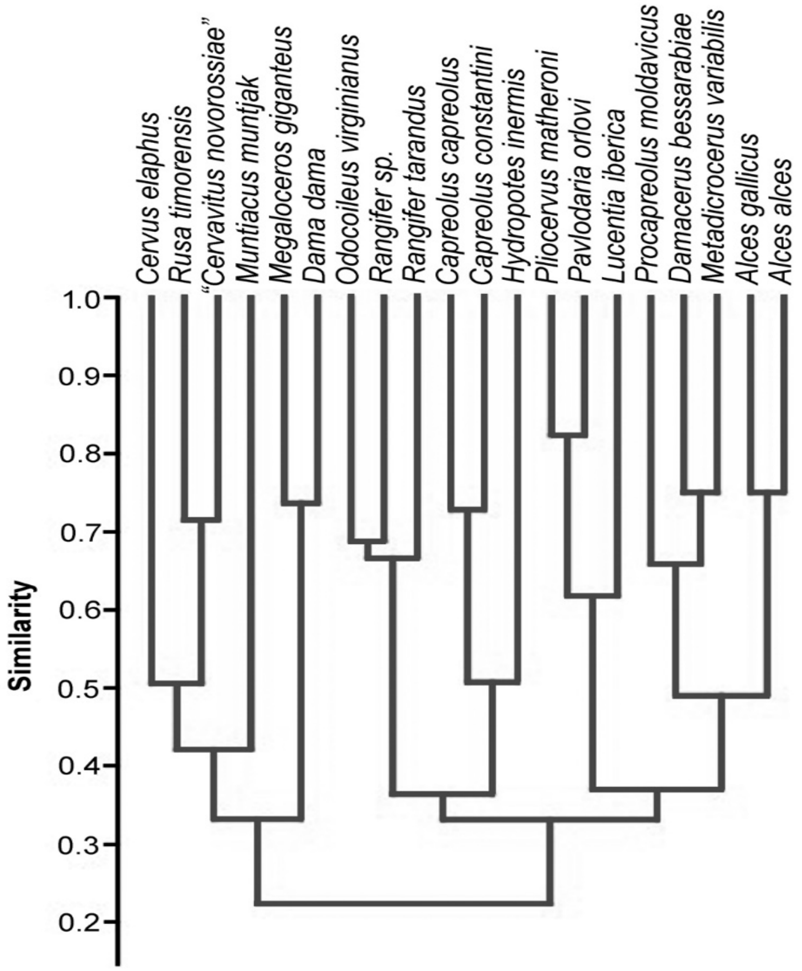

Fig. 4.2. Cluster analysis of the diagnostic antler, cranial, dental, and some postcranial characters of the Late Miocene "pliocervines" and selected modern and extinct representatives of the subfamilies Capreolinae and Cervinae. The data on "*Cervavitus novorossiae*" from the Late Tertiary of China are adapted from Zdansky (1925). The cophenetic correlation coefficient is 0.823

The analysis results reveal interesting, but expected relationships among the deer species of the subfamily Cervinae included in this study. The compared cervid species form two main clusters: the red deer group including *Cervus nestii* (Azzaroli, 1947) from the Early Pleistocene of Upper Valdarno (Italy), characterized by a narrow, wedge-shaped basioccipital, the presence of upper canines, and a pearled antler surface, and the *Axis*-*Metacervocerus*-*Dama* cluster characterized by a bell-shaped basioccipital, the loss of their canines, and a smooth antler surface.

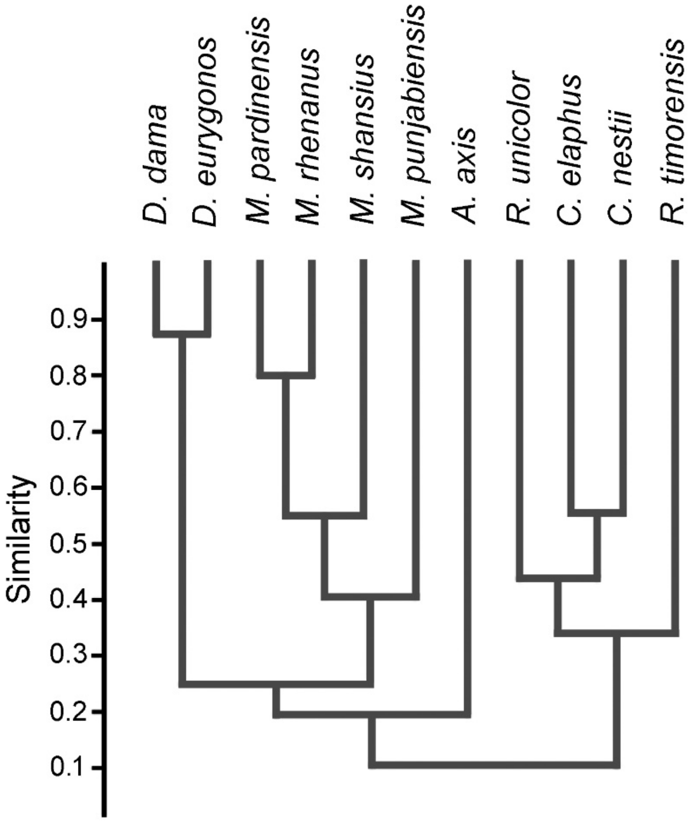

Fig. 4.3. Cluster analysis of the diagnostic cranial, dental, and antler characters of small-sized Cervinae from the Early Pleistocene of western Palearctic (the so-called "*Dama*-like deer") and selected modern and fossil cervid species from the Oriental Zoogeographic Realm. The cophenetic correlation coefficient is 0.9152

M. punjabiensis is included in the *Metacervocerus* cluster with *M. pardinensis*, *M. shansius*, and *M. rhenanus*, which confirms the systematic and apparently phylogenetic unity of those cervid forms. This result supports the inclusion of *M. punjabiensis* in the genus *Metacervocerus*, as previously proposed by Croitor and Stefaniak (2009).

The association of *Dama* with *Metacervocerus* is surprising and based on the "adaptative" antler bauplan shared by Dama and *Metacervocerus*. The apomorphic long nasal bones shared by modern *D. dama* and *M. rhenanus* do not have decisive importance, as the primitive fallow deer *D. eurygonos* is also clustered with *Metacervocerus*. Further discussion is required for the affinity identified between *Dama* and *Metacervocerus*. *Dama* is an endemic, specialized genus with a distribution restricted to the Euro-Mediterranean region that appeared in Europe during the Early Pleistocene and does not have any closely related counterparts from the paleontological record of Eastern Asia. "*Dama*" *sericus* Teilhart and Trassaert, 1937, is characterized by a completely different antler bauplan that is reminiscent of *Rucervus* (*Arvernoceros*): the trez tine is missing, the first ramification is highly situated, the angle of the first ramification is acute, and the palmation is formed by posterior crown tines, as in *R.* (*Arvernoceros*) *ardei* (Croitor, 2018a).

The earliest known fallow deer species, *D. eurygonos*, had already developed all the specialized cranial and dental features that modern fallow deer possess, with the exception of short nasal bones and missing distal palmation (Croitor, 2006b). *Metacervocerus* first appeared in Europe during the Early Pliocene (Croitor and Stefaniak, 2009). Compared to its Asian counterparts, *M. pardinensis* from the Pliocene of Europe is more advanced due to its relatively short pedicles. However, it shares similarities in dental morphology with *M. punjabiensis*, including the split lingual wall of P^2, the additional enamel fold of the protocone on the upper molars, and the inner hypoconal folding on the premolars (Heintz, 1970). The only distinguishing feature of the dentition of *M. pardinensis*, which is the type species of the genus *Metacervocerus*, is the development of the lingual cingulum on the upper molars. It is worth noting that a *Metacervocerus* specimen from the Early Villafranchian fauna of Montopoli, Italy, which is roughly contemporaneous with *M. pardinensis*, lacks cinguli in its upper molars. It is unclear if the specimen from Montopoli represents a distinct taxon or if it provides evidence that the development of cinguli is a variable character in *M. pardinensis*.

M. rhenanus, which dates back to the Early Pleistocene of Europe, lacks the cingulum on the upper molars and is characterized by advanced features such as long nasal bones (Croitor, 2006b). Therefore, we share the cautious opinion of Azzaroli (1992) that European *Metacervocerus* may belong together with *Dama* in the same stem group, although the paleontological evidence of the early evolution of this cervid stock is still missing.

The distant sister relationship between *Metacervocerus* and *Axis* suggested by our analysis is consistent with the earlier results of Bai et al. (2017) based on antler morphology and Mennecart et al. (2017) based on bony labyrinth morphology. Generally, *Metacervocerus* shows a similarity to *Axis* in the degree of evolutionary specialization. The relative length of the splanchnocranium in *M. rhenanus* (55.1%, n=2) is very close to the mean value obtained for *A. axis* (54.9%, n=4), but is also similar to the relative splanchnocranium length in *D. dama* (55.0%, n=13). *Metacervocerus* and *Axis* are characterized by similarly rounded and moderately large bullae tympani and, with the exception of *M. punjabiensis*, by a similar relative length of the neurocranium (Croitor, 2014). The difference in the development of the second antler ramification suggests that *Metacervocerus* and *Axis* acquired three-pointed antlers independently and, thus, represent two different phyletic lineages that evolved from different two-pointed antler forerunners. Unlike *Axis*, *Metacervocerus* maintains primitive features of the upper cheek teeth, such as a relatively long premolar series.

M. punjabiensis is distinguished from *A. axis* by its primitive narrow and long braincase. Interestingly, this feature is shared with *M. giganteus* and *D. dama*, and supports the results of the cluster analysis. Genetic studies have confirmed the close evolutionary relationship between *Dama* and *Megaloceros* (Lister et al., 2004). According to the data obtained by Croitor and Robinson (2020), *M. punjabiensis* shares the specific and primitive elongate proportions of the braincase found in the *Megaloceros-Dama* phylogenetic lineage. The distinctive shape of the braincase of M. punjabiensis suggests that the similarities in the braincase proportions between *A. axis* and *M. shansius* and *M. rhenanus* may be the result of evolutionary parallelism. The Late Tertiary of Eastern Asia has yielded a variety of cervines with three-pointed antlers, but their systematics and phylogenetic relationships are still unclear (Shikama, 1941; Teilhard de Chardin and Piveteau, 1930; Teilhard de Chardin and Trassaert, 1937). Future revisions of Late Tertiary plesiometacarpal deer from Eastern Asia may provide answers to questions about the phylogenetic relationships among *Metacervocerus*, *Dama*, and other related forms.

Large-sized representatives of the subfamily Cervinae. The multivariate cluster analysis of antler characters places *Megaloceros giganteus* close to *Dama*, with both species associated with the genera *Rucerus* and *Cervus* (Fig. 4.4). Contrary 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*). The results obtained also indicate that the cranial pachyostosis evolved in *Megaloceros* and *Sinomegaceros* represents a case of physiological evolutionary parallelism and does not have taxonomic value above the genus level. *M. giganteus antecedens* is the earliest form of giant deer in Europe that shows adaptations to the wooded ecosystem and is likely a specialized form of the giant deer lineage. The apparent "*Sinomegaceros*"-like antler shape of *M. giganteus antecedens* resulted from the significant shortening of antlers, which caused the coalescence of the middle and posterior tines with the distal palmation (Croitor, 2021). The analysis of antler morphology confirms the close relationship between *Megaloceros* and *Dama*, which was recently demonstrated by paleogenetic studies (Lister et al., 2005), and supports the relationship between *Rucervus* (*Arvernoceros*) *ardei* and *Rucervus duvaucelii* (Croitor, 2018a). The Late Tertiary of Eastern Asia has yielded a variety of cervines with three-pointed antlers, but their systematics and phylogenetic relationships are still unclear (Shikama, 1941; Teilhard de Chardin and Piveteau, 1930; Teilhard de Chardin and Trassaert, 1937). Future revisions of Late Tertiary plesiometacarpal deer from

Eastern Asia may provide answers to questions about the phylogenetic relationships among *Metacervocerus*, *Dama*, and other related forms.

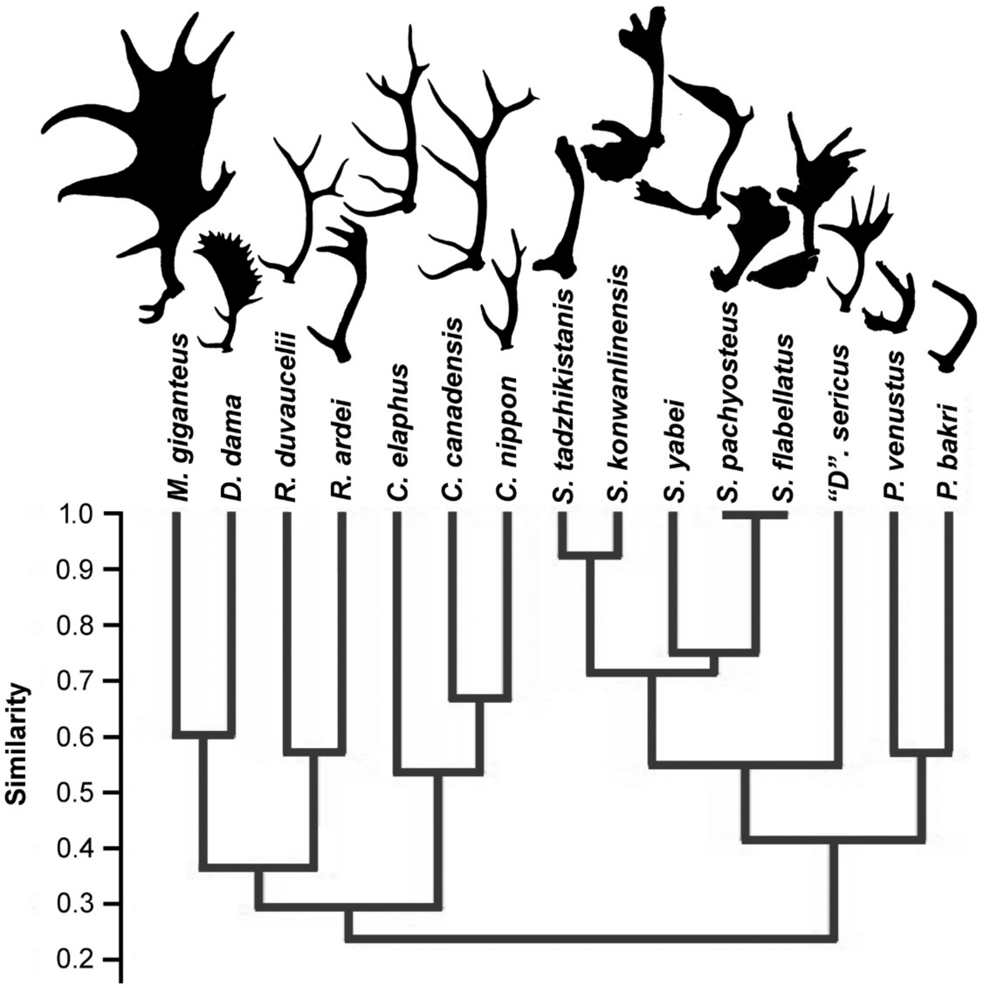

Fig. 4.4. Cluster analysis of the diagnostic antler characters combined with pachyostosis development of large-sized deer (*Megaloceros*, *Sinomegaceros*) and selected modern and extinct deer species. The cophenetic correlation is 0.8481

The *Cervus* cluster accurately represents the relationships between *C. elaphus*, *C. canadensis*, and *C. nippon*, which are consistent with genetic data (Ludt et al., 2004). However, the relationships among some genera, such as *Dama*, *Cervus*, and *Rucervus*, are not adequately resolved and do not correspond with genetic studies (Pitra et al., 2004; Gilbert et al., 2006). The poor resolution of relationships among some genera suggests that antler morphology provides useful criteria for species characterization within a genus or closely related genera but is insufficient for distantly related genera. Therefore, the results obtained confirm the importance of cranial characters as taxonomic and systematic criteria at the genus level.

5.3. Matching fossil record and molecular phylogeny data at subfamily level

The results of molecular phylogenetic analysis confirm that the subfamily Cervinae, comprising plesiometacarpal "Old World deer" with large multitined antlers, is monophyletic, which is consistent with the previously accepted viewpoint (Pitra et al., 2004). Modern molecular phylogenetic studies support the dichotomy of the family Cervidae into the informal groups of Plesiometacarpalia and Telemetacarpalia, as described by Brooke (1878) (Pitra et al., 2004; Gilbert et al., 2006). Mitochondrial and nuclear DNA analysis also supports the monophyletic nature of the subfamily Cervinae (plesiometacarpal "Old World deer") in its traditional sense (Pitra et al., 2004). Additionally, it has been shown that primitive tropical plesiometacarpal cervids with simple two-pointed antlers, which were previously included in the "primitive" subfamily Muntiacinae, are a sister phylogenetic group of cervines, and the cervine-muntiacine branch is distinct from the "New World deer" and Eurasian telemetacarpal genera *Capreolus*, *Alces*, and *Hydropotes* (Pitra et al., 2004; Gilbert et al., 2006). Therefore, the presiometacarpal type of limbs occurred only once among modern cervids.

It is likely that deer of the subfamily Cervinae independently evolved the three-pointed antler construction in several lineages. This explains the diversity of the three-pointed antler construction type, resulting from the evolution of the second tine on the anterior side of the beam (*Metacervocerus* and probably all Cervinae possessing the trez tine), or on the posterior tine (*Rucervus*). It is possible that the origin of each three-pointed antler type evolved independently in more than one lineage. Therefore, the radiation of Cervinae occurred at an earlier evolutionary stage of a cervid with two-pointed antlers.

One of the most interesting results obtained by Pitra et al. (2004) and Gilbert et al. (2006) is that the Cervinae (Muntiacini and Cervini) represent an extensive Tertiary radiation in the eastern part of the Oriental Zoogeographic province that remains intact until the present day (Geist, 1998). The western part of the Oriental Zoogeographic province remained inaccessible for Cervinae until the Early Pliocene when the Old World deer could overcome the Alpine-Himalayan Mountain belt, which acted as a limiting zoogeographic border for Cervidae during the Tertiary period (Heintz et al., 1990). "*Cervavus*" *rutmeyeri* Schlosser, 1903, "*Procapreolus*" *latifrons* Schlosser, 1924, and the holometacarpal "*Cervavitus*" *demissus* Teilhard de Chardin and Trassaert, 1937 from the Tertiary of China and Mongolia differ from European *Procapreolus* and *Damacerus* in their more robust antlers with cylindrical (not compressed from the sides) beam and tines, a comparatively low position of the first anterior tine, as well as the always absent *Palaeomeryx* fold in lower molars. These also belong to the tropical radiation of the Old World cervids.

5.4. Matching fossil record and molecular phylogeny data at genus level

The evolution of specialized phylogenetic lineages within the subfamily Cervinae that dispersed and evolved in the Palearctic zone of Eurasia is well-documented in the paleontological record. Representatives of archaic Palearctic phylogenetic branches of plesiometacarpal deer evolved adaptations to a broader range of ecological niches and colonized western Eurasia and the Indian subcontinent during the Early Pliocene (Croitor and Stefaniak, 2009; Croitor et al, 2022). The multiple dispersals of Cervinae into the Palearctic Zoogeographic Province could have resulted from repeated North to South fluctuations of the Palearctic/Oriental zoogeographic border in Eastern China, as described by Tong (2005) for the Pleistocene epoch.

Douzery and Randi (1997) suggest that the evolutionary diversification within the subfamily Cervinae is a relatively ancient event that occurred from the Mio-Pliocene boundary to the Early and Middle Pleistocene. These estimations agree with the first arrival of Cervinae (*Metacervocerus*, *Praeelaphus*, *Rucervus*) during the Early Pliocene (MN15) in Eastern Europe (Croitor and Stefaniak, 2009). Gilbert et al. (2006) confirmed that *R. duvaucelii* is grouped with the genus *Axis axis* and represents the earliest radiation of Cervinae, as previously suggested by Pitra et al. (2004). According to Pitra et al. (2004), the split between *Axis axis*, *Rucervus schomburgki*, and *R. duvaucelii* on one hand, and the remaining Cervinae on the other, is located at the base of the Cervinae phylogeny. Thus, the genera *Rucervus*, *Axis*, *Praeelaphus*, and *Metacervocerus* most likely represent the first radiation of Cervinae.

According to Douzery and Randi (1997), the initial evolutionary diversification within the phylogenetic stock leading to the genus *Cervus* occurred between 3.3 and 7.1 million years ago, while the diversification at the subspecies level within *C. elaphus* took place during 0.4-2.5 million years ago. The occurrence of *Cervus nestii* in the Early Pleistocene of Olivola (ca 2.0 Ma) and Upper Valdarno (1.7 Ma) is consistent with the estimated time of evolutionary diversification within the genus *Cervus*, as indicated by Douzery and Randy (1997). *Cervus nestii* exhibits typical cranial morphology similar to modern red deer (Croitor, 2006b). Additionally, the frontal orientation of the distal antler fork is a distinguishing characteristic shared by *C. nestii* and primitive subspecies of red deer such as *C. elaphus acoronatus*, *C. e. bactrianus*, and *C. e. yarkandensis*.

The divergence of *Dama*, the only modern genus not known from South-East Asia, from *Cervus* and related cervines from South-Eastern Asia took place early, during the Early Pliocene, estimated at around 3.0 million years ago. This finding agrees with the first occurrence of Cervinae in Western Eurasia, which likely led to the local evolution of the genus *Dama*. The most probable forerunner of *Dama* is Early Pliocene *Metacervocerus pardinensis* from Eastern Europe, characterized by simple tree-pointed antlers and a strong cingulum in upper molars. The oldest record of *Dama* comes from the Early Pleistocene of the Upper Valdarno and Val di Chiana (Italy). The cranial morphology of *D. eurygonos* from the Upper Valdarno is already advanced and does not differ from modern *D. dama*. Although the antlers of *D. eurygonos* are primitive four-pointed, they already show characteristics typical of the genus *Dama*, such as the very obtuse angle of the basal tine and the crown tine inserted on the posterior side of the antler beam.

Analysis of the cytochrome b sequence of the extinct giant deer *Megaloceros giganteus* has revealed its close phylogenetic relationship with *Dama dama* and *D. mesopotamica* (Lister et al., 2005; Hughes et al., 2006). The earliest remains of *M. giganteus* date back to about 400 kyr BP (Lister, 1994), but the estimated divergence of *Dama* and *Megaloceros* could have occurred much earlier, around 10.7 Myr ago (Hughes et al., 2006), well before the forerunner of *Dama* dispersed into western Eurasia. Unlike *Dama*, *Megaloceros* is characterized by a more primitive cranial morphology, expressed in a less flexed braincase and less vertical position of pedicles. The evolution of *Megaloceros giganteus* lineage took place in the dry woodlands with more or less condinental climate of Eastern Europe and Western Siberia.

The results of hierarchical cluster analysis of craniodental characters of fallow deer and giant deer confirm their evolutionary relationship and place them close to *Metacervocerus* (Croitor, 2021). *Megaceroides algericus* from the Late Pleistocene and Holocene of North Africa is morphologically similar to *M. giganteus* (Croitor, 2016). The little-known "*Dama mesopotamica*" *mugarensis* di Stefano 1996 from the Late Middle Pleistocene of Tabun (Middle East) is another interesting deer from the Mediterranean Area. This medium-sized cervid strongly resembles *Megaloceros* with its flattened bifurcated basal tine, significantly flattened antler beam, and the presence of cingulum in upper molars. The cervid from Tabun appears soon after the dispersal of *Megaloceros* in Europe and possibly belongs to the *Megaloceros*-*Megaceroides* stock and is a direct forerunner of *M. algericus*. *M. algericus* is an interesting example of adaptation to an ecological niche (periaquatic or semiaquatic herbivore) where a cervid could avoid ecological competition with African bovids.

According to Douzery and Randy (1997), the Capreolinae clade may have originated between 8.7 and 10.4 million years ago (Ma). This estimate is consistent with the stratigraphic 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). Like Cervinae, the Late Miocene radiation of Capreolinae included a range of ecological and evolutionary forms, including *Metadicrocerus* with large palmed antlers and the hog-deer-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. Although holometacarpal limbs with advanced reduction of proximal portions of lateral metacarpals are known for *Metadicrocerus* (Croitor, 2021), the holometaparpality of other Late Miocene cervids from Eastern Europe has not been demonstrated yet (Azanza et al., 2013). The earliest finding of *Capreolus* in Udunga, Trans-Baikal area of Russia (Vislobokova et al., 1995) suggests that the origin of roe deer occurred in the eastern part of Palearctic.

The origin of *Alces* could be related to a cervid similar to *Metadicrocerus variabilis*, which is characterized by short and comparatively stronger divergent pedicles and large antlers that tend to evolve palmations. The time of divergence of Capreolini+Alceini (7.4 Ma) according to Gilbert et al. (2006) corresponds to the occurrence of *Metadicrocerus* in Vallesian-Turolian of Moldova (MN 10-12, 7.1-9.5 Ma) (Petronio et al., 2007; Dong, 2011).

5.5. Conclusions to Chapter 5

1) Deer antlers primarily serve as a means of intraspecific communication between males during the rutting period, through combats and displays. However, antler evolution can also be influenced by other factors that indirectly affect communication. Larger body mass increases the risk of fatal combats, which has led to the development of protective basal and middle tines. The posterior tine has evolved in several deer lineages adapted to open landscapes as an adaptation against ectoparasites that weaken males and reduce their vigilance during the rutting period (Croitor, 2020).

2) Small "*Dama*-like" deer, often included in the genus *Pseudodama* Azzaroli, 1992, belong to different modern and extinct genera, including *Cervus*, *Dama*, *Metacervocerus*, and *Praeelaphus* (Croitor, 2006b; Croitor and Robinson, 2020).

3) Craniodental diagnostic characters confirm the close relationship between *Megaloceros*, *Dama*, and *Praedama*. The evolutionary relationship between *Dama* and *Megaloceros*, revealed by molecular phylogeny data, agrees with the results of the cluster analysis of craniodental characters (Croitor, 2021). However, the supposed close relationship between *Megaloceros* and *Sinomegaceros* is not supported by antler morphology (Croitor, 2021; Croitor et al., 2021).

4) The estimated evolutionary divergence between Cervinae and Capreolinae, based on molecular phylogeny data, agrees with the occurrence of archaic Capriolinae in Late Miocene Europe (Croitor, 2014; 2021).

5) Cervid forms from the Late Neogene of the eastern Palearctic reported as "*Cervavitus novorossiae*" do not exhibit morphological features of capreolines and require systematic revision (Croitor, 2021).

6) *Metacervocerus*, *Rucervus* (*Arvernoceros*) and *Praeelaphus*, from the Early Pliocene of Eastern Europe, represent the early evolutionary radiation of Cervinae that occurred in Southeast Asia (Croitor, 2018b).

7) The chronology of the evolutionary divergence of *Dama*, based on molecular phylogeny data, corresponds to the arrival of the first "*Dama*-like" deer of the genus *Metacervocerus* in western Eurasia (Croitor and Robinson, 2020).

6. PALEOBIOGEOGRAPHY OF DEER FROM THE WESTERN PALEARCTIC

6.1. Paleobiogeography of subfamily Capreolinae

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

The paleobiogeographic history of telemetacarpal and plesiometacarpal deer may explain the differences between Capreolinae and Cervinae. The evolutionary radiation of telemetacarpal deer in western Eurasia occurred in the conditions of the Mediterranean biome, which emerged 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, according to Allen (1996) and Rundel et al. (2016), may have caused this transition. Unlike cervines, capreolines did not have extensive refugia within the tropical climate latitudes, and all their evolutionary radiation occurred in rather dry Mediterranean-type biomes. The telemetacarpal type of lateral metacarpal reduction is possibly linked to the cursorial adaptation in relatively dry environments with hard ground, where the maintained articulations of lateral digits with the preserved distal portions of the second and fifth metacarpals could be an adaptation preventing their displacement and wounding.

The earliest known representatives of the subfamily Capreolinae are reported from the Late Miocene sites of Otovasca 1 (MN9, Moldova) and Răspopeni (MN10, Moldova) as *Procapreolus* sp. and *Cervavitus* sp. respectively (Lungu and Rzebik-Kowalska, 2011). A diversified group of primitive capreolines also exists from the Late Miocene of the Iberian Peninsula. This group of archaic Capreolinae is represented by a small-sized muntjac-like deer ("Muntiacinae gen et sp. indet.") from the Late Miocene site of Creventille-2 (Spain) (Croitor, 2021). The cervid from Creventille-2 was as large as modern barking deer; however, it is characterized by relatively narrower and higher upper molars when compared to Asian muntjacs (Croitor et al., 2020). Deer of the genus *Lucentia* (*L. iberica* and *L. pierensis*) from the Late Miocene of the Iberian Peninsula

(MN11) are somewhat larger but maintain the primitive two-pointed antlers with a very high position of bifurcation (Azanza, 2000).

The next stage of capreoline evolution is characterized by three-pointed antlers, which are represented by the genus *Procapreolus*. *Procapreolus* had the most diversified evolutionary radiation among the early capreolines, with at least nine species, and dispersed as far as eastern regions of Eurasia (Croitor et al., 2020). The evolutionary radiation of *Procapreolus* is marked by the rather uniform shape of three-pointed lyre-shaped antlers and various combinations of advanced and primitive characteristics of dentition. *Procapreolus* maintained an archaic feature of large upper canines (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, as 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 evolve a small distal palmation, *D. bessarabiae* maintains primitive features of dentition, such as the unmolarized lower fourth premolar and the strong *Palaeomeryx* fold in lower molars. The next stage of evolution is represented by *Metadicrocerus variabiilis*, which maintained the basic three-pointed antler bauplan but evolved multiple tine bifurcations of its palmated antlers. It is worth noting that a similar way of evolving multi-tined palmated antlers is assumed for *Alces* (Bubenik, 1990).

The earliest known cervid fossil with the frontal bone shape characteristic of elk, featuring a sideward orientation of the pedicle, comes from the Pliocene of Udunga in the Trans-Baikal Area (Vislobokova et al., 1995). The oldest known *A. gallicus* remains come from the Middle Villafranchian of Navrukho (Tajikistan) and Livenzovka (Azov Sea Area of Russia) (Vislobokova, 1986; Nikolsky and Titov, 2002). Eurasian fossil elks are generally considered chronospecies of a single phyletic lineage with gradual increases in body size and shortening of antler beams (Azzaroli, 1953; Heintz and Poplin, 1980; Lister, 1987; Breda and Marchetti, 2005; Nikolsky, 2010). However, the Pleistocene European elk species are likely to be specialized side branches, such as *A. gallicus*, which has an extremely evolved antler morphology and a very large antler span caused by elongation of the basal segment of the antler. Out of all species in the *Alces* genus, *A. gallicus* has the most specialized antlers and is the most divergent from the initial capreoline antler bauplan. Nevertheless, some features (*Palaeomeryx* fold, unmolarized P_3, long nasal bones) are still primitive. The relatively short braincase of *A. gallicus* suggests that it is an advanced elk form that likely represents a side evolutionary branch that dispersed to Western Europe, with river meadows in the temperate open plains of Asia serving as the probable ecosystem where it evolved. The unmolarized P_3 of North American *Cervalces scotti* and Eurasian *A. gallicus* indicate that these species belong to the first successful evolutionary radiation of elks, preceding the P_3 molarization process observed in *Alces latifrons*. *A. latifrons*, in its turn, is distinguished by its elongated braincase, cannot be directly linked to European *A. gallicus*, suggesting that *A. latifrons* evolved in Asia and replaced *A. gallicus* during the early Middle Pleistocene (Croitor, 2918b).

The origin of *Rangifer* is believed to be related to the middle latitudes of Siberia as well. 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 suggests that Northern Eurasia may be a possible center of reindeer origin (Bondarev et al., 2017). The specimen from Isakovka-4 is characterized by the typical reindeer frontoparietal suture and the short and broad braincase. The pedicles, unlike those of modern reindeer, are inclined backwards and set parallel to each other, demonstrating the primitive cervid morphological condition. The associated fauna and flora indicate rather warm climate 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 with the advanced American barren-ground caribou. This has 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 immigration event of reindeer in Eurasia occurred during the Riss Glaciation. While there is a genetic gap between the North American forest caribou and barren ground caribou, the genetic distance between the tundra subspecies *R. tarandus tarandus* and the forest subspecies *R. tarandus fennicus* is not as large (Geist, 1988). Based on mitochondrial DNA analysis, the modern Eurasian tundra and forest subspecies have a diphyletic origin from a smaller refugium in western Eurasia situated in close connection to the extensive ice sheet that covered Fennoscandia, and a larger refugium of Beringia (Røed, 2005).

The paleontological record does not contradict genetic data: apparently, the origin of the fossil reindeer with relatively small teeth known as "*R. tarandus guettardi*" took place 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 mixed with local European reindeer forms (Croitor, 2010).

Rankama and Ukkonen (2001) suggest that Western Europe is the area of origin of modern tundra reindeer. Unlike fossil *Rangifer*, modern subspecies of Eurasian reindeer are concentrate feeders with small cheek teeth and reduced lower incisors and canines that do not participate in food gathering (modern reindeer take the forage by their lips) and have an enlarged nasal cavity representing an adaptation to breathing cold and dry air (Flerov, 1952; Sokolov, 1959). Specific adaptations of *R. tarandus fennicus* to forest habitats evolved after forest extension in the postglacial time and have a secondary character (Geist, 1998; Røed, 2005). According to Rankama and Ukkonen (2001), the origin of forest reindeer could be related to the forested refugium in the East from Fennoscandia. This hypothesis finds its support in Alekseeva (1990), who mentioned a finding of a fossil reindeer skull from Tatarstan (Russia) similar to modern *R. tarandus fennicus*.

6.2. Dispersals and paleobiogeography of Cervinae in western Eurasia

Cervines have undergone an evolutionary radiation that is zoogeographically compact and primarily centered in the eastern part of the Oriental zoogeographic province, remaining generally intact until the present day (Geist, 1998). The subfamily Cervinae, as currently understood (including Muntiacini and Cervini) proposed by Grubb (2000) and confirmed by genetic studies (Pitra et al., 2004; Gilbert et al., 2006), represents a broad Late Neogene radiation from the most primitive *Muntiacus* and *Elaphodus* with simple antlers and large upper tusks to the larger *Rucervus*, which evolved complicated richly branched antlers (*Rucervus schomburgki*). Unlike the subfamily Capreolinae, which represents an evolutionary radiation of telemetacarpal deer in the temperate latitudes of western Eurasia, the subfamily Cervinae represents a southern Oriental radiation of plesiometacarpal deer that took place in tropical latitudes. The eastern part of the Oriental zoogeographic province is the area of highest diversification of the subfamily Cervinae and the hypothetical center of the initial radiation of plesiometacarpal deer (Geist, 1998; Di Stefano and Petronio, 2002; Croitor, 2014).

During most of the Neogene, the dispersal of Cervinae was restricted to the eastern part of the Oriental zoogeographic province because the Alpine-Himalayan mountain belt and the climate gradient toward the north created effective zoogeographic borders for the Cervines (Heintz et al., 1990). The Indian subcontinent, as well as western Eurasia, were colonized by plesiometacarpal deer almost simultaneously during the Pliocene (Croitor et al., 2021).

The overview of Late Miocene cervids from western Eurasia demonstrates a remarkable absence of deer belonging to the subfamily Cervinae. The first representatives of this subfamily appear in the Early Pliocene faunas of Eastern Europe and belong to three different genera with varying degrees of evolutionary specializations: *Praeelaphus australorientalis*, *P. warthae*, *Metacervocerus pardinensis*, and *Rucervus* (*Arvernoceros*) *ardei* (Croitor and Stefaniak, 2009). These enlisted species took their origin from the first important Late Miocene radiation of

Cervinae, which is currently represented by *Axis axis* and *Rucervus duvaucelii* from South-East Asia (Pitra et al., 2004).

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

The lineage of *Rucervus* survived in the Iberian glacial refugium as the endemic specialized form *Haploidoceros mediterraneus* until the Late Pleistocene. New data on antler morphology provided by remains of *H. mediterraneus* retrieved from Cova del Rinoceront suggest that this species belongs to the phylogenetic stock of *Rucervus* (*Arvernoceros*). This conclusion is based on the presence of vestigial or atavistic posterior crown tine in the antlered skull CR-6189, combined with cranial morphology, which is consistent with this phylogenetic relationship (Croitor et al., 2020).

The dental morphology and 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 cingulum in 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 masticatory apparatus of *H. mediterraneus* represents several superimposed morphological adaptations that resulted in an unusual combination of morphological features: relatively large cheek teeth and narrow, pointed premaxillary bones, as seen in browsing herbivores. *H. mediterraneus* from Cova del Rinoceront was the last representative of the long-lasting *R.* (*Arvernoceros*)–*Haploidoceros* lineage, which went extinct during the Late Pleistocene when modern fallow deer dispersed into the Iberian Peninsula. Late Pleistocene fallow deer from Iberia are known to exist in the context of temperate interglacial faunas (Álvarez-Lao et al., 2013). It can be assumed that Late Pleistocene *D. dama* was an ecologically more flexible faunal immigrant on the Iberian Peninsula, competing with local *H. mediterraneus* for the same resources. It is important to note that *H. mediterraneus* evolved in the geographically isolated Iberian glacial refugium, which had no direct geographic contact with geographically interconnected Italian, Balkan, and Anatolian refugia. The paleobiogeographic isolation of the Iberian glacial refugium allows us to presume that *H. mediterraneus* was poorly adapted to the resource competition with faunal invaders from the oriental glacial refugia. The competitive exclusion of *H. mediterraneus*, caused by the dispersal of modern fallow deer in combination with climate change, is the most plausible reason for the extinction of this Iberian Pliocene faunal holdover.

The genus *Praeelaphus* is a phylogenetic lineage of plesiometacarpal deer that appeared in the Early Pleistocene of Europe and has had a long evolutionary history in the western Palearctic. *Praeelaphus* is represented in western Eurasia by several forms distinguished by body size and some details in antler morphology. Deer of the genus *Praeelaphus* are characterized by primitive dental morphology. However, the length of the braincase in *Praeelaphus* is relatively short, while four-pointed antlers are rather specialized in their 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 rather 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 the 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 the conditions of insular isolation. *Praeelaphus messinae* is characterized by roe-deer-like body size and some features of antlers (such as the flattened area of antler ramification and the pyriform beam cross-section) that are characteristic of continental *Praeelaphus*.

The shape of the basioccipital is a useful taxonomic criterion within the plesiometacarpal Cervinae. The narrow V-shaped basioccipital is characteristic of *Cervus elaphus*, but it is also present in other species such as *Muntiacus muntjak*, *Panolia eldii*, *Rucervus unicolor*, and *Elaphurus davidianus* (Croitor, 2014). It can even be observed in the skull of *Przewalskium albirostris* illustrated by Flerov (1952: fig. 40). According to the results of genetic analyses by Pitra et al. (2004) and Gilbert et al. (2006), *C. elaphus*, *E. davidianus*, *P. albirostris*, *P. eldii*, and

R. unicolor form a single phylogenetic group, and thus these authors suggest including these modern species in the genus *Cervus sensu stricto*.

The broadened basioccipital pharyngeal tuberosities are shared by *Praeelaphus australorientalis*, *P. warthae*, and *P.* cf. *lyra* from Olivola, suggesting that this archaic European lineage likely diverged very early from the *Cervus* phylogenetic branch. The same shape of the basioccipital bone is also found in *Axis axis*, *R. duvaucelii*, and *Dama dama*, as well as in most extinct European genera such as *Metacervocerus*, *Arvernoceros*, *Eucladoceros*, *Praemegaceros*, and *Megaloceros* (Croitor, 2014). Genetic analysis has shown that *A. axis* and *R. duvaucelii* split from the main stock of Cervinae very early (Pitra et al., 2004) and represent the earliest radiation of Cervinae along with *Praeelaphus*, *Arvernoceros*, and *Metacervocerus* (Croitor, 2014). Unlike *Dama*, *P. australorientalis* is characterized by small bullae tympani with an irregular shape (an ancestral character) and a relatively short and broader braincase (an advanced character). Therefore, the cranial morphology of *P. australorientalis* and fallow deer represents two different and mutually exclusive directions of specialization

The relative length of the braincase, the shape of the basioccipital, and the relative length of pedicles are characteristics that bring *P. australorientalis* closer to *M. rhenanus*. However, *M. rhenanus*, a cervid with larger rounded bullae tympani and simple three-pointed antlers with a cylindrical beam (which has a regularly circular transversal section), is distinct from *P. australorientalis*. Furthermore, even if we assume that the advanced morphology of *P. australorientalis'* antlers is a result of parallel evolution of closely related lineages, its antlers do not show morphological homology with those of *M. rhenanus* or *M. pardinensis*. The second tine in *P. australorientalis* is located very close to the first tine and does not resemble the distal bifurcation in *Metacervocerus*. Nevertheless, it is possible that *Praeelaphus* and *Metacervocerus* are relatively closely related, as they may represent consecutive stages of evolutionary specialization of antlers resulting from the same evolutionary radiation event.

Cervus nestii represents the earliest dispersal event of the genus *Cervus* in the Western Palearctic. This small cervid is characterized by the typical modern red deer cranial morphology. The frontal orientation of the distal antler fork is another specific characteristic shared by *C. nestii* and the primitive extinct and modern subspecies of red deer, including *C. elaphus acoronatus* that spread across western Eurasia in the early Middle Pleistocene. The local evolution of red deer in western Eurasia produced a wide variety of subspecies and forms during the Middle and Late Pleistocene. This diversity of forms most probably resulted 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 interesting from a paleozoogeographic point of view since it had broader connections with the Balkan Peninsula during the glacial periods and acted as a part of the Balkan-Italian glacial refugium. The geographic isolation of the Italian Peninsula during the interglacial periods caused the partial isolation of local red deer populations that created the conditions for the local evolution of forms such 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 (Croitor and Obada, 2018). *C. canadensis* and *C. elaphus* are vicariant species, based on 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 (Croitor, 2020). 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* Azzaroli (Croitor, 2020).

The tribe Megalocerotini *sensu lato* (Vislobokova, 1990, 2013) is a polyphyletic group in its traditional understanding. The tribe Megalocerotini Brookes, 1828, *sensu stricto*, with the genera *Praedama*, *Megaloceros*, *Megaceroides*, and *Dama*, represents a monophyletic phylogenetic branch that radiated in the western part of Eurasia. However, the present state of knowledge does not provide a satisfactory diagnosis for this restricted group of genera containing extremely specialized forms.

The cervid forms grouped under the terms "giant deer" or "large-sized deer" represent several lineages that evolved similar convergent adaptations, such as large body size and complicated palmated antlers, in similar conditions, i.e., open relatively dry woodlands 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, 2006a, 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 the extreme distribution range for Cervinae in the cold middle latitudes of Eurasia. *Sinomegaceros pachyosteus* is another pachyostotic cervine species that may have been affected by the repeatedly advancing arid zones of Central Asia.

Megaloceros giganteus and *Dama dama* share some primitive characteristics, such as the relatively long braincase and short orbitofrontal portion of the skull, as well as some derived characteristics like the long nasal bones that extend beyond the imaginary line connecting the anterior edges of the orbits. However, unlike *Dama*, *Megaloceros* retained primitive characteristics such as the slightly flexed braincase and a rather oblique position of the pedicles on the skull. The differences in antler morphology suggest that *Megaloceros* and *Dama* evolved their crown part of antlers independently and in distinct ways. In fallow deer, including the earliest known species *D. eurygonos* from the Early Pleistocene of Italy, the crown tines are inserted on the posterior side of the beam, whereas *D. clactoniana* developed crown tines on both the anterior and posterior sides of the beam, representing an exceptional derived feature among *Dama*. The anterior crown tine may occasionally evolve in *D. mesopotamica*, but the development of supplementary occasional prongs in different parts of the antlers is a characteristic feature of this species (Di Stefano, 1996). In *M. giganteus*, the crown tines are inserted only on the anterior side of the beam and fringe the distal end of palmation. The differences in antler morphology confirm a relatively distant phylogenetic relationship between *M. giganteus* and modern fallow deer, which took place before the evolutionary transition from three-tined to four-tined antlers (Croitor, 2021).

The phylogenetic relationship between *R. ardei* and *M. giganteus*, as assumed by Heintz (1970), conflicts with important features such as the general antler bauplan and the relative length of the braincase. Unlike *M. giganteus*, the crown part in *R. ardei* is composed of crown tines inserted on the posterior side of the beam (Croitor, 2018a). Additionally, *R. ardei* is characterized by the relatively short braincase, an advanced feature not present in *M. giganteus*, which maintains relatively long primitive proportions of the braincase (Croitor, 2018b). The basal tine with the additional prong in *R. ardei* is not homologous to the bifurcated and flattened basal tine of *M. giganteus*. In giant deer, the range of ontogenetic and individual variation of the basal tine shape passes through simple flattening without bifurcation, known as the "spoon-shaped" basal tine. This "transitional" variant is not present in *R. ardei* (Croitor, 2021). The craniodental characters and antler bauplan of *R. ardei* approach it to modern *R. duvaucelii* (Croitor, 2018a, b).

According to Azzaroli (1953, 1994), the flattened shape of the basal tine shared by *Praedama savini* and *M. giganteus* may indicate a close phylogenetic relationship between them. Some authors (Vislobokova, 1990, 2012, 2013; van der Made and Tong, 2008; van der Made, 2014, 2018) accept this viewpoint, but they do not provide additional arguments. The complete antler of *Praedama* from the late Middle Pleistocene of Pinedo, Spain (Aguado, 1962), is of particular interest because it is characterized by the bauplan that may be considered as initial for the *Praedama* lineage and shows a striking similarity with the antler bauplan of *M. giganteus*. The crown portion of the antlers from Pinedo has a peculiar comb-like construction with four crown tines. Crown tines 1 and 2 (Fig. A.41) are homologous with the anterior crown tines in *M. giganteus*, while the two distal-most crown tines are homologous with the distal crown tines in *M.*

giganteus. Thus, the hypothesis of Azzaroli (1953, 1994) on close phylogenetic relationship of *Praedama* and *Megaloceros* is supported by the results of the present study.

The *Megaloceros-Praedama-Dama* phylogenetic branch is likely related to the genus *Metacervocerus*, which dispersed from Southeast Asia to Europe during the Early Pleistocene (Croitor, 2021). Several species of *Metacervocerus* with simple three-tined antlers were present during the Pliocene and Early Pleistocene of Eurasia. Some 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 giant deer.

The origin of the *Megaloceros* phylogenetic branch is related to the open wooded habitats of southwestern Siberia and northern Kazakhstan, which represent the core area of giant deer evolution and geographic distribution. *Praedama* is a side evolutionary branch of the *Megaloceros* lineage that dispersed into Europe by the end of the Villafranchian. Early representatives of *Praedama* already possess the antler bauplan typical for *Megaloceros* and show 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 general evolutionary specialization was maintained in most Eurasian giant deer forms.

Following the Pleistocene climate fluctuations, *M. giganteus* repeatedly dispersed into Western Europe 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, *Megaloceros mugharensis* (Di Stefano, 1996) from the Middle Pleistocene of the Near East, and *Megaceroides algericus* (Lydekker, 1890) from the Late Pleistocene-early Holocene of North Africa. Therefore, *Megaloceros* represents one of the few exceptional cases of cervids colonizing North Africa, possibly due to their physiological capacity to tolerate the brief seasonal shortage of food supply (Croitor, 2016). The extreme evolutionary plasticity of giant deer antlers refutes the long-held views on their large antlers as a harmful overspecialization that caused the extinction of *M. giganteus*.

The genus *Praemegaceros* represents another lineage of large-sized deer that evolved a set of morphological features convergent with *Megaloceros*. The oldest species of this genus, *Praemegaceros obscurus*, is reported from Dmanisi, dated back to 1.81 Ma (Vekua et al., 2010), suggesting a South Asian origin for the species. The origin of *P. obscurus* should be sought in the paleontological record of the Sivalik Hills. Most of the antler characters of *Panolia* sp. from the Siwalik Hills, including 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 *P. obscurus*. Therefore, it can be assumed that *P. obscurus* is a large-sized descendant of *Panolia* sp. from the Siwaliks.

The Cretan endemic genus *Candiacervus* is related to continental *Praemegaceros*. The genus is represented by several dwarfed species that show various degrees of evolutionary antler simplification and specialization (van der Geer, 2018). The less specialized species *Candiacervus devosi* van der Geer, 2018 is characterized by a specific antler bauplan and the presence of all structural elements of antlers, including the dorsal tine, the middle tine, and the posterior tine, indicating a direct evolutionary relationship with a continental form of *Praemegaceros* (*P. obscurus* or *P. verticornis*).

6.3. Conclusions to Chapter 6

1) Following the mass extinction of archaic Late Miocene Capreolinae in western Eurasia, only a few lineages of telemetacarpal deer survived in the eastern part of the Palearctic (*Capreolus*, *Alces*, *Rangifer*, *Hydropotes*). All these lineages are represented by arctic, boreal, and middle latitude forms (Croitor, 2021).

2) The dispersal of Pliocene Cervinae into western Eurasia was an important event that defined the modern biogeographic distribution of cervid subfamilies in Eurasia. The earliest representatives of the subfamily Cervinae from Europe are related to the modern genera *Axis* and *Rucervus* from the Oriental biogeographic realm (Croitor and Stefaniak, 2009).

3) The first occurrence of the modern Palearctic genera *Cervus* and *Dama* is recorded in the Early Pleistocene of Europe and the Caucasian region (Croitor, 2006b).

4) The tribe Megalocerotini sensu lato is polyphyletic and includes cervid forms that belong to three distinct phylogenetic branches: *Rucervus* (*Arvernoceros*) *ardei*, which belongs to the early evolutionary radiation of *Cervinae*; *Megaloceros*, *Megaceroides*, *Praedama*, and *Dama*, which represent a phylogenetic radiation that took place in the western part of Eurasia (Megalocerotini *sensu stricto*); and the genus *Praemegaceros*, which is related to the *Cervus elaphus* evolutionary stock (Croitor, 2016, 2018b).

5) The extinction of most Pleistocene Cervinae was caused by the ecological opportunism specific to this ruminant group and their low degree of feeding specialization. Such an ecological strategy makes plesiometacarpal deer good colonizers of new ecosystems but rather weak competitors with other ruminants, including cervids (Croitor, 2018b).

CONCLUSIONS AND RECOMMENDATIONS

1. Each of the modern cervid subfamilies, Cervinae and Capreolinae, resulted from ancient (Late Miocene) adaptive radiations that occurred in two different zoogeographic provinces: the eastern part of the Oriental province and the Palearctic province, respectively. Cervinae (Muntiacini+Cervini) represent a broad Tertiary adaptive radiation in the eastern part of the Oriental Zoogeographic province, which remains generally intact until the present. The majority of phylogenetical lineages of Cervinae, which became extinct during the Plio-Pleistocene (such as *Eucladoceros*, *Praemegaceros*, *Arvernoceros*, *Praeelaphus*, *Megaloceros*, etc.), had a temperate and boreal latitude distribution.

2. The tribe Megalocerotini Brookes, 1828 (= Megacerini Viret, 1961) *sensu lato* is now considered polyphyletic, as it includes forms of cervids that belong to three distinct phylogenetic branches. *Rucervus* (*Arvernoceros*) *ardei* is part of the early evolutionary radiation of Cervinae. *Megaloceros*, *Megaceroides*, and *Praedama*, along with the genus *Dama*, form a phylogenetic radiation that occurred in the western part of Eurasia (known as Megalocerotini sensu stricto). Finally, the genus *Praemegaceros* is related to the *Panolia* - *Cervus* phylogenetic branch.

3. In contrast to Cervinae, the modern Eurasian Capreolinae phylogenetic clade has experienced significant depletion. The Late Miocene *Pliocervus matheroni* from Mont Luberon (France) is closely related to *Pavlodaria orlovi* from Kazakhstan and therefore belongs in Capreolinae. The subfamily Pliocervinae Symeonidis, 1974 is synonymous with Capreolinae Brookes, 1828, and the tribe Pliocervini Symeonidis, 1974 should be included in the subfamily Capreolinae and limited to the genera *Pliocervus* and *Pavlodaria*.

4. The genus *Cervavitus*, as traditionally understood, is polyphyletic. Taxonomic analysis demonstrated that *Cervavitus s.s.* is a junior synonym of *Damacerus*, a monotypic genus from the Late Miocene of Southeastern Europe. Both *Damacerus bessarabiae* Khomenko, 2013 and *Metadicrocerus variabilis* (Khomenko, 2013) belong to the early evolutionary radiation of the telemetacarpal deer, which is a subfamily of Capreolinae that evolved during the Late Miocene of Europe. *M. variabilis* represents an early evolutionary stage of the telemetacarpal condition and is characterized by Capreolinae-specific traits such as the general plan of antler construction, the relatively long lower premolar series, the advanced molarization of P_4, and the presence of the *Palaeomeryx* fold in lower molars. The *Palaeomeryx* fold is a diagnostic feature of archaic Capreolinae. The genus *Lucentia* represents the most primitive two-pointed stage of antler evolution in Capreolinae.

BIBLIOGRAPHY

1. ABBAZZI, L. *Megaceroides obscurus* from the Val di Chiana (Cava Liberatori, Tuscany, Central Italy, f.u., early Pleistocene). Remarks on the early evolution and systematical of *Megaceroides*. *Bollettino della Società Paleontologica Italiana*, 1995a, nr. 34(2), pp. 223-234. ISSN 0375-7633.
2. ABBAZZI, L. Occurrence of palmated *Cervus elaphus* from Italian late Pleistocene localities. *Rendiconti Lincei, Scienze Fisiche e Naturali, Serie IX*, 1995b, nr. 6(3), pp. 189-206. ISSN 2037-4631.
3. ABBAZZI, L. Remarks on the validity of the generic name *Praemegaceros* Portis 1920, and an overview on *Praemegaceros* species in Italy. *Rendiconti Lincei*, 2004, nr. 15(2), pp. 115-132. ISSN 2037-4631.
4. ABBAZZI, L., BONFIGLIO, L., MARRA, AC., MASINI, F. A revision of medium and small sized deer from the Middle and Late Pleistocene of Calabria and Sicily. *Bolletino della Societa Paleontologica Italiana*, 2001, nr. 40 (2), pp. 115-126. ISSN 0375-7633.
5. ABBAZZI, L., CROITOR, R. *Eostyloceros* cf. *pidoplitschkoi* Korotkevitsch, 1964 (Cervidae, Muntiacinae): new element in the Neogene mammal assemblage of Lower Valdarno (Tuscany, Central Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 2003, nr. 109(3), pp. 575-580. ISSN 0035-6883.
6. ABBAZZI, L., FICCARELLI, G., TORRE, D. Deer Fauna from the Aulla quarry (Val di Magra, Northern Apennines). Biochronological remarks. *Rivista Italiana di Paleontologia e Stratigrafia*, 1995, nr. 101(3), pp. 341-348. ISSN 0035-6883.
7. ABBAZZI, L., MASINI, F. *Megaceroides solilhacus* and other deer from the middle Pleistocene site of Isernia La Pineta (Molise, Italy). *Bollettino della Societa Paleontologica Italiana*, 1996, nr. 35 (2), pp. 213-227. ISSN 03757633.
8. ABDRAKHMANOVA, LT. Fossil ruminants of Karabastuz. *Materials on History of Fauna and Flora of Kazakhstan*, 1974, nr. 6, pp. 83-89 (in Russian).
9. AHLÉN I. Studies on the red deer, *Cervus elaphus* L., in Scandinavia. 1. History of distribution. *Swedish Wildlife*, 1965, nr. 3, pp. 1–88.
10. AGUADO, MM. El hombre primitivo en Toledo. *Toletum: boletín de la Real Academia de Bellas Artes y Ciencias Históricas de Toledo*, 1962, nr. 3, pp. 175-206.
11. ALCALDE, GM., VAN DEN HOEK OSTENDE, LW. Above the hoof: functional morphology of the fossil deer from Tegelen, the Netherlands. *Geological Journal*, 2015, nr. 50(3), pp. 271-289. ISSN 1099-1034.
12. ALDROVANDI, U. *Quadrupedum omnium bisulcorum historia*. Bologna, 1621, 1040 p.

13. ALEKPEROVA NA. 1964. A finding of a new for Azerbaidjan deer *Cervus* (*Rusa*) *sp.* from Upper Pliocene deposits. *Bulletin of the Academy of Sciences of Azerbaidjan SSR, geological-geographical series*, nr. 2, pp. 59-62.
14. ALEKSEJEV, A.K. About new form of deer from the neighborhood of village Petroverovka. *Notes of the Novorossiysk Society of Naturalists*, 1913, nr. 40, pp. 1-13 (in Russian).
15. ALEKSEJEV, A.K. *Animaux fossiles du village Novo-Elisavetovka*. Tehnik, Odessa: 1915. 346 p. (in Russian).
16. ALEKSEEVA, EV. *Mammals from Pleistocene of South-East of Western Siberia*. Nauka, Leningrad: 1980. 187 p. (in Russian).
17. ALEKSEEVA LI. Theriofauna of Eastern Europe Early Anthropogene. *Transactions of Geological Institute*, 1977, nr. 300, pp. 3-108 (in Russian).
18. ALEKSEEVA, LI. Upper Pleistocene Theriofauna of Eastern Europe. *Transactions of Geological Institute*, 1990, nr. 455, pp. 1-110 (in Russian).
19. ALESSANDRI, DE G. Sopra alcuni avanzi di cervidi pliocenici del Piemonte. *Atti Rendiconti dell' Accademia Reale delle Scienze di Torino*, 1903, nr. 1902-1903, pp. 2-17.
20. ALLEN, HD. Mediterranian environments. In: ADAMS, WM., GOUDIE AS., ORME AR., Eds. *The Physical Geography of Africa*. Oxford: Oxford University Press, 1996, pp. 307–325.
21. ALLEN, JA. The mountain caribou of Northern British Columbia. *Bulletin of the American Museum of Natural History*, 1900, nr. 13, pp. 1-18.
22. ALLEN, GM. Pigs and deer from the Asiatic expeditions. *American Museum Novitates*, 1930, nr. 430, pp. 1-19.
23. ÁLVAREZ-LAO, DJ., ARSUAGA, JL., BAQUEDANO, E., PÉREZ-GONZÁLEZ, A. Last Interglacial (MIS 5) ungulate assemblage from the Central Iberian Peninsula: The Camino Cave (Pinilla del Valle, Madrid, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2013, nr. 374, pp. 327-337. ISSN 0031-0182.
24. AMBROSETTI, P. Cromerian Fauna of the Rome Area. *Quaternaria*, 1967, nr. 9, pp. 267-283.
25. AMSON, E., KOLB, C., SCHEYER, TM., SÁNCHEZ-VILLAGRA, MR. Growth and life history of Middle Miocene deer (Mammalia, Cervidae) based on bone histology. *Comptes Rendus Palevol*, 2015, nr. 14(8), pp.637-645. ISSN 16310683.

26. APOSTOL, L. L'étude morphométrique des mammifères fossiles quaternaires de la Plain Roumain et leur distribution paléo-zoogéographique. *Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa"*, 1976, nr. 17, pp. 341-375.
27. ARAMBOURG, C. Note préliminaire sur une nouvelle grotte à ossements des environs d'Alger. *Bulletin Societe Histoire Naturelle Afrique du Nord*, 1932, nr. 23, pp. 154-162.
28. ARAMBOURG, C. Mammifères fossiles du Maroc. Mèmoires Société Sciences Naturelles Maroc, 1938, nr. 46, pp. 1-74.
29. AUBEKEROVA, PA. Pliocene artiodactyls of southeastern Kazakhstan. *Paleontological Journal*, 1974, nr. 4, pp. 92-100 (in Russian).
30. AUJARD-CATOT, R., CREGUT, E., GAGNIERE, S., GRUNEISEN, A., MOURER-CHAUVIRE, C. Un squelette complet de renne, *Rangifer tarandus* (Mammalia, Artiodactyla), dans le Pleistocene superieur du remplissage karstique de l'Aven des Planes (Monieux, Vaucluse, France). *Nouv. Arch. Musee d'Histoire naturelle*, 1979, nr. 17 (suppl.), pp. 15-20. ISSN 0766-7248.
31. AZANZA, B. The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). Cervidae (Artiodactyla, Mammalia). *Münchner Geowissenschaftliche Abhandlungen (A)*, 1995, nr. 28, pp. 157-166. ISSN 0177-0950.
32. AZANZA, B. Los Cervidae (Artiodactyla, Mammalia) del Mioceno de las Cuencas del Duero, Tajo, Calatayud-Teruel y Levance. *Memorias del Museo Paleontológico de la Universidad de Zaragoza*, 2000, nr. 8, pp. 1-376. ISSN 0214-2023.
33. AZANZA, B., MONTOYA, P. A new deer from the lower Turolian of Spain. *Journal of Paleontology*, 1995, 69(6), pp. 1163-1175. ISSN 0022-3360.
34. AZANZA, B., RÖSSNER, GE., ORTIZ-JAUREGUIZAR, E. The early Turolian (late Miocene) Cervidae (Artiodactyla, Mammalia) from the fossil site of Dorn-Dürkheim 1 (Germany) and implications on the origin of crown cervids. *Palaeobiodiversity and Palaeoenvironments*, 2013, nr. 93(2), pp. 217-258. ISSN 1867-1594.
35. AZZAROLI, A. I cervi fossili della Toscana. *Palaeontographia Italica*, 1947, nr. 43, pp. 46-81.
36. AZZAROLI, A. L'alce di Sénèze. *Palaeontographia Italica*, 1952, nr. 47, pp. 133-141.
37. AZZAROLI, A. The Deer of the Weybourn Crag and Forest Bed of Norfolk. *Bulletin of the British Museum (Natural History), Geology*, 1953, nr. 2(1), pp. 3-96.
38. AZZAROLI, A. Critical observations upon Siwalik Deer. *Proceedings of the Linnaean Society of London*, 1954, nr. 165, pp. 75-83.

39. AZZAROLI, A. Il nanismo nei cervi insulari. *Palaeontographia Italica*, 1961, nr. 26, pp. 1-31.
40. AZZAROLI, A. A skull of the Giant Deer *Megaceros verticornis* from Eastern Tuscany. *Rendiconti Lincei, scienze fisiche e naturali Accademia dei Lincei*, 1976, nr. 61(6), pp. 485-487. ISSN 2037-4631.
41. AZZAROLI, A. Taxonomy of Quaternary Alcini (Cervidae, Mammalia). *Acta Zoologica Fennica*, 1985, nr. 170, pp. 179-180. ISSN 0001-7299
42. AZZAROLI, A. Critical Remarks on some Giant Deer (genus *Megaceros* Owen) from the Pleistocene of Europe. *Palaeontographia Italica*, 1979, nr. 41, pp. 5-16. ISSN 0373-0972.
43. AZZAROLI, A. The cervid genus *Pseudodama* n. g. in the Villafranchian of Tuscany. *Palaeontographia Italica*, 1992, nr.79, pp. 1-41. ISSN 0373-0972.
44. AZZAROLI, A. Forest Bed elks and giant deer revisited. *Zoological Journal of the Linnean Society*, 1994, nr. 112(1-2), pp. 119-133. ISSN 0024-4082.
45. AZZAROLI, A., MAZZA, P. The cervid genus *Eucladoceros* in the early Pleistocene of Tuscany. *Palaeontographia Italica*, 1992a, nr. 79, pp. 43-100. ISSN 0373-0972.
46. AZZAROLI, A., MAZZA, P. On the possible origin of the Giant Deer of genus *Megaceroides*. *Rendiconti Lincei. Scienze fisiche e naturali*, 1992b, nr. 9(3), pp. 23-32. ISSN 2037-4631.
47. AZZAROLI, A., MAZZA, P. Large early Pleistocene deer from Pietrafitta lignite mine, Central Italy. *Palaeontographia Italica*, 1993, nr. 80, pp. 1-24. ISSN 0373-0972.
48. BAYGUSHEVA, VS. On skull construction of the large-sized deer of the Khaprovian mammal assemblage. In: TATARINOV, LP., ed. *Paleoteriologia*, Moscow: Nauka, 1994, pp. 236-252 (in Russian). ISBN 5-02-005723-1.
49. BAYGUSHEVA, V., TITOV, V. Pleistocene large mammal associations of the Sea of Azov and adjacent regions. In: TITOV, V., TESAKOV, A., eds. *Quaternary stratigraphy and paleontology of the Southern Russia: connections between Europe, Africa and Asia: Abstracts of the International INQUA/SEQS Conference (Rostov-on-Don, June 21–26, 2010)*. Rostov-on-Don, 2010, pp. 24-27. ISBN 978-5-902 982-83-8.
50. BAYGUSHEVA, VS., TITOV, VV. Large deer from the Villafranchian of Eastern Europe (Sea of Azov Region): Evolution and paleoecology. *Quaternary International,* 2013, nr. 284, pp. 110-122. ISSN 1040-6182.
51. BARKER, R. An Account of a Stag's Head and Horns, Found at Alport, in the Parish of Youlgreave, in the County of Derby. In a Letter from the Rev. Robert Barker, BD to John

Jebb, MDFRS. *Philosophical Transactions of the Royal Society of London,* 1785, nr. 75, pp. 353-355.

52. BARRAL, L., SIMONE, S. *Préhistoire de la Côte d'Azur orientale. Imprimerie nationale de Monaco*. Monaco, 1968. 136 p.
53. BELAN, N. G. Late Pleistocene Reindeer from Dniepr Area. *Vestnik Zoologii,* 1983, 5, pp. 20-26 (in Russian). ISSN 2073-2333, 0084-5604.
54. BELGRAND, E. *La Seine: I. Le bassin parisien aux âges antéhistoriques*. Paris: Imprimerie nationale, 1883. 50 p.
55. BELLUCCI, L., SARDELLA, R., ROOK, L. Large mammal biochronology framework in Europe at Jaramillo: the Epivillafranchian as a formal biochron. *Quaternary International*, 2015, 389, pp. 84-89. ISSN 1040-6182.
56. BERCKHEMER, F. Über die Riesenhirschfunde von Steinheim an der Murr. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, 1941, nr. 96, pp. 63-88.
57. BLUMENBACH, J. *Handbuch der naturgeschichte. Vol. 16*. Göttingen: Johann Christian Dieterich, 1799. 697 p.
58. BONDAREV, AA., TESAKOV, AS. SIMAKOVA, AN., DOROGOV, AL. 2017. Reindeer (*Rangifer*) from Early Pleistocene of the South of Western Siberia. In: BOGDANOVA, TN. et al. eds. *Integrative Palaeontology: Development Prospects for Geological Objectives, Material of the LXIII Session of the Palaeontological Society (April, 3-7, 1917, Sankt-Peterburg)*, pp. 173-175 (in Russian). ISBN 978-5-904247-99-7.
59. BOESKOROV, GG. *The systematics and origin of the modern moose*. Novosibirsk: Nauka, 2001. 120 p. (in Russian). ISBN 5-02-030441-7.
60. BONIFAY, MF. Principales formes caracteristiques du quarternaire moyen du sud-est de la France (Grands Mamiferes). *Bulletin du musee d'antropologie prehistorique de Monaco*, 1967, nr.14, pp. 49-62.
61. BONIFAY, MF. Carnivores quaternaires du Sud-Est de la France. *Memoires du Museum national d'histoire naturelle, Serie C*, 1971, 21(2), pp. 1-377.
62. BONIFAY MF. Interet des etudes taphonomiques au Pleistocene ancient: Soleilhac et Seyssaguet (Blanzac, Haute-Loire). *Bulletin du Muséum national d'Histoire naturelle, Paris*, 4e ser., 1986, nr. 8, pp. 269-281. ISSN 0012-9615.
63. BOUCHUD, J. *Essai sur le renne et la climatologie du Paléolithique moyen et supérieur.* Périgueux: Imprimerie Magne, 1966. 300 p.

64. BOUCHUD, J. Étude d’un crâne de renne fossile (« *Rangifer guettardi* » Desmarest) découvert dans le sud de la France. Problèmes actuals de paléontologie (Evolution des vertébrés) *Colloque International C. N. R. S.*, 1967, nr. 163, pp. 557-568.
65. BOUT, P., AZZAROLI, A. Stratigraphie et Faune du creux de Peirolles pres Perrier (Puy-de-Dôme). *Annales de Paléontologie*, 1952, nr. 38, pp. 3-22.
66. BOUVRAIN, G., DE BONIS, L. April. Ruminants (Mammalia, Artiodactyla: Tragulidae, Cervidae, Bovidae) des gisements du Miocène supérieur (Turolien) de Dytiko (Grèce). *Annales de Paléontologie*, 2007, nr. 93 (2), pp. 121-147. ISSN 0753-3969.
67. BOUVRAIN, G., GERAADS, D., JEHENNE, Y. Nouvelles donees relatives a la classification des Cervidae (Artiodactyla, Mammalia). *Zoologischer Anzeiger*, 1989, nr. 223(1-2), pp. 82-90. ISSN 0044-5231.
68. BREDA, M. The holotype of *Cervalces gallicus* (Azzaroli, 1952) from Sénèze (Haute-Loire, France) with nomenclatural implications and taxonomical-phylogenetic accounts. *Rivista Italiana di Paleontologia e Stratigrafia*, 2001, nr. 107(3), pp. 439-449. ISSN 0035-6883.
69. BREDA, M., LISTER, AM. *Dama roberti*, a new species of deer from the early Middle Pleistocene of Europe, and the origins of modern fallow deer. *Quaternary Science Reviews*, 2013, nr. 69, pp. 155-167. ISSN 0277-3791.
70. BREDA, M., LISTER, A., KAHLKE, RD. New results on cervids from the Early Pleistocene site of Untermassfeld. In: KAHLKE, RD., ed. The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany), Part 4. *Monographien des Römisch-Germanisches Zentralmuseum*, 2020, nr. 40(4): pp. 1197-1249, Mainz: Verlag des Römisch-Germanischen Zentralmuseums. ISBN 978-3-88467-347-8.
71. BREDA, M, MARCHETTI, M. Systematical and biochronological review of Plio-Pleistocene Alceini (Cervidae; Mammalia) from Eurasia. *Quaternary Science Reviews*, 2005, nr. 24, pp. 775-805. ISSN 0277-3791.
72. BRISSON MJ. Regnum Animale in classes IX distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species. Parisiis (Bauche), 1756. 382 p.
73. BROOKE, V. On the Classification of the Cervidae with the synopsis of the existing Species. *Proceedings of the Zoological Society of London*, 1878, nr. 46(1), pp. 883-928.
74. BROOKES, J. Brookesian Museum: A Prodromus of a Synopsis Animalium, Comprising a Catalogue Raisonné, of the Zootomical Collection of Joshua Brookes. Part 1. A

Catalogue of the Anatomical and Zoological Museum. London: Gold and Walton, 1828. 76 p.

75. BUBENIK, AB. Epigenetical, Morphological, Physiological, and Behavioral Aspects of Evolution of Horns, Pronghorns, and Antlers. In: BUBENIK, GA., BUBENIK, AB. Eds. *Horns, Pronghorns, and Antlers*. New York: Springer-Verlag, 1990. pp. 3-113. ISBN: 978-1-4613-8966-8.
76. BUKHSIANIDZE, M. Dmanisi artiodactyl assemblage. In: HOLWERDA, F., MADERN, A., VOETEN, D., VAN HETEREN, A., MEIJER, H., DEN OUDEN, N., eds. *XIV Annual Meeting of the European Association of Vertebrate Palaeontologists, 6-10 July 2016, Programme and Abstract Book*. Haarlem, 2016, p. 37.
77. CALOI, L., MALATESTA, A. Il Cervo Pleistocenico di Sardegna. *Memorie dell'Istituto Italiano di Paleontologia Umana*, 1974, nr. 2, pp. 162-247.
78. CALOI, L., PALOMBO, M.-R. *Megaceros solilhacus* Robert, da Terranera (bacino di Venosa, Potenza). *Quaternaria*, 1979, nr. 21, pp. 129-138. ISSN: 2300-0384.
79. CALOI, L., PALOMBO, M.-R. *Megaceros savini* e *Megaceros* cf. *verticornis* (Cervidae) del Pleistocene medio-inferiore di Ponte Galeria (Roma). *Geologica Romana,* 1980, nr. 19, pp. 121-130. ISSN 0435-3927.
80. CALOI, L., PALOMBO, MR. Functional aspects and ecological implications in Pleistocene endemic herbivores of Mediterranean Islands. *Historical Biology*, 1994, nr. 8(1-4), pp.151-172. ISSN: 0891-2963.
81. CAPASSO BARBATO, L. Les cervidés endémiques de Crète. *Quaternaire*, 1990, nr. 1 (3-4), pp. 265-270. ISSN 1965-0795.
82. CAPASSO BARBATO, L. Nuova specie di cervide del Pleistocene di Creta. *Atti della Accademia Nazionale dei Lincei, Scienze Fisiche e Naturale*, 1992, Serie IX, nr. 1 (7), pp. 183-220. ISSN 1720-0768.
83. CARTE, A. On the remains of reindeer which have been found fossil in Ireland. *Journal of Geological Society of Dublin*, 1864, nr. 10, pp. 103-107.
84. COLUCCI, AP. Pseudodama farnetensis *piccolo cervide del tardo Villafranchiano proveniente dai riempimenti carsici dell'area fra Apricena e Poggio Imperiale (Fg)*. Ph.D. Thesis in Natural Sciences, University of Bari, 1993, 86 p.
85. COMASCHI CARIA, I. Resti di Cervidi nel Quaternario di Porto Vesme (Sardegna sud-occidentale). *Rivista Italiana di Stratigrafia e Paleontologia*, 1955, nr. 55, pp. 17-22.
86. COMASCHI CARIA, I. Specie nuova di Cervo nel Quaternario di Alghero (Sardegna). *Rendiconti Seminario Facoltà di Schienze, Università di Cagliari*, 1956, nr. 25, pp. 1-6.

87. COMASCHI CARIA, I. Nuovi resti di Cervidi nel Pleistocene della Sardegna. *Comunicazione presentata al V Congresso Internazionale INQUA*, 1957, pp. 1-10.
88. CREGUT-BONNOURE, E., TSOUKALA, E. The Pliocene Artiodactyla and Proboscidea (Mammalia) from Gephyra (lower Axios valley, Macedonia, Greece). Discovery of a new boselaphine. *Quaternary International*, 2017, nr. 445, pp. 200-214. ISSN 1040-6182.
89. CROITOR, R. On Systematic Position of "moldavian sambar deer" from the Pliocene of Moldova. *Bollettino Della Societa Paleontologica Italiana*, 1999, nr. 38(1), pp. 87-96. ISSN 0375-7633.
90. CROITOR, R. Functional morphology of small-sized deer from the early and middle Pleistocene of Italy: implication to the paleolandscape reconstruction. In: CAVARRETTA, G., GIOIA, P., MUSSI, M., PALOMBO, MR., eds. *Proceedings of the 1st International Congress "The World of Elephants", Roma, 16-20 ottobre*. Rome: Consignio Nazionale delle Ricerche, 2001, pp. 97-102. ISBN 88-8080-025-6.
91. CROITOR, R. Systematics and phylogeny of large-sized deer of the genus *Praemegaceros* Portis, 1920 (Cervidae, Mammalia). In: *Late Neogene and Quarternary biodiversity and evolution: Regional developments and interregional correlations. 18th International Senckenberg Conference – VI International Palaeontological Colloquium in Weimar, 2004*. Weimar, 2004, pp. 89-90. ISSN 0946-8978, ISBN 3-00-013600-2.
92. CROITOR, R. Large-sized deer from the early Pleistocene of South-east Europe. *Acta Palaeontologica Romaniae*, 2005, nr. 4, pp. 97-104. ISSN 1842-371x.
93. CROITOR, R. Taxonomy and systematics of large-sized deer of the genus *Praemegaceros* Portis, 1920 (Cervidae, Mammalia). In: KAHLKE, RD., MAUL, LC., MAZZA, PPA., eds. Late Neogene and Quaternary biodiversity and evolution: Regional developments and interregional correlations. Volume I. *Courier Forsch.-Institut Senckenberg*, 2006a, 256: 91-116. ISSN 0341-4116.
94. CROITOR, R. Early Pleistocene small-sized deer of Europe. *Hellenic Journal of Geosciences*, 2006b, nr. 41, pp. 89-117. ISSN 1105-0004.
95. CROITOR, R. Systematical position and evolution of the genus *Arvernoceros* (Cervidae, Mammalia) from Plio-Pleistocene of Eurasia. *Oltenia. Studii şi comunicări. Ştiinţele Naturii*, 2009, nr. 25, pp. 375-382. ISSN 1454-6914.
96. CROITOR, R. The History of Reindeer in the Paleolithic of Moldova. *Stratum Plus*, 2010, nr. 1, pp. 137-165 (in Russian). ISSN 1857-3533, 1608-9057.
97. CROITOR, R. Lower Pleistocene ruminants from Monte Riccio (Tarquinia, Italy). *Oltenia. Studii şi conumicări. Ştiinţele naturii*, 2012, nr. 28(1), pp. 221-226. ISSN 1454-6914.

98. CROITOR, R. Deer from Late Miocene to Pleistocene of Western Palearctic: matching fossil record and molecular phylogeny data. *Zitteliana B*, 2014, nr. 32, pp. 115-153. ISSN 1612-4138.

99. CROITOR, R., 2016. Systematical position and paleoecology of the endemic deer *Megaceroides algericus* Lydekker, 1890 (Cervidae, Mammalia) from the late Pleistocene-early Holocene of North Africa. *Geobios*, 49(4), pp. 265-283. ISSN 0016-6995.

100. CROITOR, R. Description of a new deer species (Cervidae, Mammalia) from the Early Pliocene of Eastern Europe, with a review of early dispersals and palaeobiogeography of the subfamily Cervinae. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 2017, nr. 283(1), pp. 85-108. ISSN 00777749.

101. CROITOR, R. A description of two new species of the genus *Rucervus* (Cervidae, Mammalia) from the Early Pleistocene of Southeast Europe, with comments on Hominin and South Asian ruminants dispersals. *Quaternary*, 2018a, 1(2), 17, https://doi.org/10.3390/quat1020017. ISSN: 2571-550X.

102. CROITOR, R. *Plio-Pleistocene Deer of Western Palearctic: Taxonomy, Systematics, Phylogeny*. Chișinău: Institute of Zoology of the Academy of Sciences of Moldova: 2018b. 139 p. ISBN 978-9975-66-609-1.

103. CROITOR, R. A new form of wapiti *Cervus canadensis* Erxleben, 1777 (Cervidae, Mammalia) from the Late Pleistocene of France. *Palaeoworld*, 2020, nr. 29(4), pp.789-806. ISSN 1871-174X.

104. CROITOR, R. Early evolutionary radiation and diversity of the Old World telemetacarpal deer (Capreolinae, Cervidae, Mammalia). *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, 2021a, nr. 300(1), pp.33-67. ISSN 0077-7749.

105. CROITOR, R. Taxonomy, systematics and evolution of giant deer *Megaloceros giganteus* (Blumenbach, 1799) (Cervidae, Mammalia) from the Pleistocene of Eurasia. *Quaternary*, 2021, nr. 4(4), pp. 36. ISSN 2571-550X.

106. CROITOR, R., ABBAS, SG., BABAR, MA., KHAN, MA. A new deer species (Cervidae, Mammalia) from the upper Siwaliks (Pakistan). *Quaternary International*, 2021, nr. 595, pp. 1-11. ISSN 1040-6182.

107. CROITOR, R., BONIFAY, MF. Étude préliminaire des cerfs du gisement Pleistocène inférieur de Ceyssaguet (Haut-Loire). *Paleo*, 2001, nr. 13, pp. 129-144. ISSN 2101-0420.

108. CROITOR, R., BONIFAY, MF., BONIFAY, E. Origin and evolution of the late Pleistocene island deer *Praemegaceros* (*Nesoleipoceros*) *cazioti* (Depéret) from Corsica

and Sardinia. *Bulletin du Musée d'anthropologie préhistorique de Monaco*, 2006, nr. 46, pp. 35-68. ISSN 0544-7631.

109. CROITOR, R., COJOCARU, I. An antlered skull of a subfossil red deer, *Cervus elaphus* L., 1758 (Mammalia: Cervidae), from Eastern Romania. *Acta Zoologica Bulgarica*, 2016, nr. 68(3), pp.407-414. ISSN 0324-0770.

110. CROITOR, R., OBADA, T. On the presence of Late Pleistocene wapiti, *Cervus canadensis* Erxleben, 1777 (Cervidae, Mammalia) in the Paleolithic site Climăuți II (Moldova). *Contributions to Zoology*, 2018, nr. 87(1), pp. 1-10. ISSN 1383-4517.

111. CROITOR, R., KOSTOPOULOS, DS. On the systematic position of the large-sized deer from Apollonia, Early Pleistocene, Greece. *Paläontologische Zeitschrift*, 2004, nr. 78(1), pp. 137-159. ISSN 0031-0220.

112. CROITOR, R., ROBINSON, C. A revision of "*Cervus*" *punjabiensis* Brown, 1926 (Cervidae, Mammalia) from the Upper Siwaliks of Chandigarh, India. *Quaternary International*, 2020, nr. 550, pp.147-158. ISSN: 1040-6182.

113. CROITOR, R., STEFANIAK, K. Early Pliocene deer of Central and Eastern European regions and inferred phylogenetic relationships. *Palaeontographica*, 2009, nr. 287, pp. 1-39. ISSN 0375-0442.

114. CROITOR, R., STEFANIAK, K., PAWŁOWSKA, K., RIDUSH, B., WOJTAL, P., STACH, M. Giant deer *Megaloceros giganteus* Blumenbach, 1799 (Cervidae, Mammalia) from Palaeolithic of Eastern Europe. *Quaternary International*, 2014, nr. 326-327, pp. 91-104. ISSN 1040-6182.

115. CROITOR, R., ZAKHAROV, D., MARARESCUL, V. Deer from the early pliocene prioziornoe, kuchurgan river valley (Moldova, Eastern Europe). *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, 2020, nr. 297(3), pp.325-367. ISSN 0077-7749.

116. CROIZET, J., JOBERT, A. *Recherches sur les ossements fossils du Département du Puy de Dôme*. Paris, 1828. 226 p.

117. CURRAN, SC. Expanding ecomorphological methods: geometric morphometric analysis of Cervidae post-crania. *Journal of Archaeological Science*, 2012, nr. 39, p. 1172-1182. ISSN 0305-4403.

118. CURRAN, SC. Exploring *Eucladoceros* ecomorphology using geometric morphometrics. *The Anatomical Record*, 2015, nr. 298(1), pp. 291-313. ISSN 1932-8486.

119. CUVIER, G. *Recherches sur les ossements fossiles. Tome quatrieme*. Paris: Dufour et D'Ocagne, 1823. 514 p.

120. CUVIER, G., GRIFFITH, E., SMITH, CH. H., PIDGEON, E., GRAY, JE., GRAY, G. R. *The Animal Kingdom. Volume the fifth: Synopsis of the species of the class Mammalia*. London: William Clowes, 1827, 391 p.

121. CZYŻEWSKA, T. *Cervus* (*Rusa*) *sp*. z plioceńskiej brekcji kostnej z Wężow. *Acta Palaeontologica Polonica*, 1959, nr. 4(4), pp. 389-429.

122. CZYZEWSKA, T. Nouvelle espece de cervide du genre *Cervoceros* Khomenko de la breche pliocene de Węże pres de Dzialoszyn. *Acta Palaeontologica Polonica*, 1960, nr. 5(3), pp. 283-318.

123. CZYŻEWSKA, T. Deer from Węże and their relationship with the Pliocene and Recent Eurasiatic Cervidae. *Acta Palaeontologica Polonica*, 1968, nr. 8(4), pp. 537-593.

124. DAMES, HW. Hirsche und Mäuse von Pikermi in Attica. *Zeitschrift der Deutschen geologischen Gesellschaft*, 1883, nr. 35, pp. 92-100.

125. DANILKIN, AA. *Deer (Cervidae). Mammals of Russia and adjacent regions*. Moscow: Geos Publishing House, 1999, 552 p. (in Russian). ISBN 5-89118-092-8.

126. DAMES, W. Hirsche und Mäuse von Pikermi in Attica. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 1883, nr. 35(1), pp.92-100.

127. DAVID, A. A new deer species (Cervidae, Mammalia) from the late Pliocene deposits of Moldova (in Russian). *Buletinul Academiei de Ştiinţe din Republica Moldova. Seria Ştiinţelor Chimice şi Biologice*, 1992, nr. 1, pp. 67-68. ISSN 2284-7995.

128. DAVID, AI., SHUSHPANOV, KI. Mammal remains from the Neogene deposits of Moldavia. In: David, AI, Negadaev-Nikonov, KN., Ganea, IM., Danici, MM. (Eds.), *Vertbrates of Neogene and Pleistocene of Moldavia*, Chișinău: Știința, 1972, pp. 3-18 (in Russian).

129. DAVITASHVILI, L. *The theory of sexual selection*. Moscow: Academy of Sciences of USSR, 1961. 538 p.

130. DAWKINS, WB. On a new species of deer from the Norwich Crag. *Quarterly Journal of the Geological Society*, 1868, nr. 24(1-2), pp.516-519.

131. DAWKINS, WB. On the Cervidae of the Forest-bed of Norfolk and Suffolk. *Quaternary Journal of the Geological Society of London*, 1872, nr. 28, pp. 405-410.

132. DAWKINS, WB. Contributions to the history of the Deer of the European Miocene and Pliocene strata. *Quaterly Journal of Geological Society*, 1878, nr. 34, pp. 402-420.

133. DAWKINS, WB. The British Pleistocene Mammalia. Part 6: British Pleistocene Cervidae. *Palaeontographical Society*, 1887, nr. 40, pp. 1-29.

134. DE GIULI, C. Late Villafranchian Faunas in Italy: the Selvella Local Fauna in the southern Chiana Valley – Umbria. *Palaeontographia Italica*, 1986, nr. 74, pp. 11-50. ISSN 0373-0972.

135. DE GREGORIO A. Mammiferi quaternari di Sicilia. Parte III: sui genere *Cervus*. *Annali del Museo di Scienze Naturali di Palermo*, 1925, nr. 40, pp. 1-17.

136. DEGUSTA, D., VRBA, E. Methods for inferring paleohabitats from discrete traits of the bovid postcranial skeleton. *Journal of Archaeological Science*, 2005a, nr. 32(7), pp. 1115-1123. ISSN 0305-4403.

137. DEGUSTA, D., VRBA, E. Methods for inferring paleohabitats from the functional morphology of bovid phalanges. *Journal of Archaeological Science*, 2005b, nr. 32(7), pp. 1099-1113. ISSN 0305-4403.

138. DE LUMLEY, H., KAHLKE, HD., MOIGNE, AM., MOULLE, PE. Les faunes de grands mammiferes de la grotte du Vallonnet Roquebrune-Cap-Martin, Alpes-Maritimes. *L'Anthropologie*, 1988, nr. 92(2), pp. 465-496. ISSN 0003-5521.

139. DENK, T., GRIMM, GW., GRÍMSSON, F., ZETTER, R.,. Evidence from "Köppen signatures" of fossil plant assemblages for effective heat transport of Gulf Stream to subarctic North Atlantic during Miocene cooling. *Biogeosciences*, 2013, nr. 10(12), pp. 7927–7942. ISSN 1726-4170.

140. DEPERET, Ch. Nouvelles études sur les Ruminants pliocènes et quaternaires d'Auvergne. *Bulletin de la Société Géologique de France*, 1884, nr. 3(12), pp. 247-284.

141. DEPERET, Ch. Les animaux pliocènes du Roussillon. *Mémoires de la Société Géologique de France*, 1890, nr. 3, pp. 5-194.

142. DEPERET, C. Etude de quelques gisements nouveaux de Vertébrés pléistocènes de l'île de Corce. *Annales Societe Linnéenne Lyon*, 1897, nr. 44(1), pp. 111-128.

143. DEPERET, C., MAYET, L. Le gisement de Senèze et sa faune paléomammalogique. *Association Française pour l'avancement des Sciences, Comptes Rendus 39e Session, Toulouse 1910. Notes et Mémoires,* 1910, nr. 1911, pp. 261-263.

144. DE SERRES, M. *Geognosie des terraines tertiaires ou Tableau des principales animaux invertebrees des terrains marins tertiates du midi de la France*. Montpellier, 1829. 377 p.

145. DESMAREST, AG. *Tableau encyclopédique méthodique. Mammalogie, 2e part*. Paris, 1822. 447 pp.

146. DE STEFANO, G. I mammiferi preistorici dell'Imolese. *Palaeontographia Italica*, 1911, nr. 17, pp. 49-139.

147. DIETRICH, WO. Zur Kenntnis der oberpliocaenen echten Hirsche. *Zeitschrift de Deutschen Geologischen Gezellschaft*, 1938, nr. 90(5), pp. 261-267.

148. DI STEFANO, G. The mesopotamian fallow deer (*Dama*, Artiodactyla) in the Middle East Pleistocene. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, 1996, nr. 199(3), pp. 295-322. ISSN 0077-7749.

149. DI STEFANO, G., PANDOLFI, L., PETRONIO, C., SALARI, L. The morphometry and the occurrence of *Cervus elaphus* (Mammalia, Cervidae) from the Late Pleistocene of the Italian Peninsula. *Rivista Italiana di Paleontologia e Stratigrafia*, 2015, nr. 121(1), pp. 103-120. ISSN 0035-6883.

150. DI STEFANO, G., PETRONIO, C. A new *Cervus elaphus* subspecies of Middle Pleistocene age. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, 1992, nr. 190(1), pp. 1-18. ISSN 0077-7749.

151. DI STEFANO, G., PETRONIO, C. Origin and evolution of the European fallow deer (*Dama*, Pleistocene). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 1997, nr. 203(1), pp. 57-75. ISSN 0077-7749.

152. DI STEFANO, G., PETRONIO, C. Origin of and relationships among the *Dama*-like cervids in Europe. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 1998, nr. 207(1), pp. 37-55. ISSN 0077-7749.

153. DI STEFANO, G., PETRONIO, C. Systematics and evolution of the Eurasian Plio-Pleistocene tribe Cervini (Artiodactyla, Mammalia). *Geologica Romana*, 2002, nr. 36, pp. 311-334. ISSN 0435-3927.

154. DONG, W. Les Cervidae (Artiodactyla) rusciniens (Pliocene) du Languedoc et du Roussilion (France). *Bulletin du Museum national d'Histoire naturelle, 4^{e} ser., Section C*, 1996, nr. 18(1), pp. 133-163. ISSN 0181-0642.

155. DONG, W. Reconsideration of the systematics of the Early Pleistocene Cervavitus (Cervidae, Artiodactyla, Mammalia). *Estudios Geológicos*, 2011, nr. 67(2), pp. 603-611. ISSN 0367-0449.

156. DONG, W., PAN, Y., LIU, J. The earliest *Muntiacus* (Artiodactyla, Mammalia) from the Late Miocene of Yanmou, southwestern China. *Comptes Rendus Palevol*, 2004, nr. 3, pp. 379-386. ISSN 1631-0683.

157. DONG, W., YE, J. A morphological analysis of intraspecific variation of *Cervavitus novorossiae*. *Acta Palaeontologica Sinica*, 1997, nr. 36 (2), pp. 253-269. ISSN: 0001-6616.

158. DOUZERY, E, RANDI, E. The Mitochondrial Control Region of Cervidae: Evolutionary Patterns and Phylogenetic Content. *Molecular Biology and Evolution*, 1997, nr. 14 (11), pp. 1154-1166. ISSN 0737-4038.

159. DRIESCH, A. VON DEN. A guide to the measurements to animal bones from archaeological sites. Peabody Museum Bulletin. Cambridge (MA): Harvard University, 1976, pp. 1-137. ISBN 0-87365-950-3.

160. DUBOIS, E. On an equivalent of the Cromer Forest-bed in the Netherlands. *Koninklijke Akademie van Wetenschappen, Proceedings, Section of Sciences*, 1904, nr. 7(3), pp. 214-222.

161. EREMIA, A. Arealul toponimic Cahul. Microtoponimia localităților rurale. *Philologia*, 2011, nr. 5-6, pp. 106-122. ISSN 2587-3717.

162. ERXLEBEN, ICP. *Systema regni animalis per classes, ordines, genera, species, varietates: cum synonymia et historia animalium: Classis I. Mammalia*. Lipsiae: Impensis Weygandianis, 1777, xlviii + 636 p.

163. ERMOLOVA, N. *Anthropogene theriofauna of Angara Valley*. Novosibirsk: Nauka, 1978, 222 p. (in Russian). ISBN 13-04-07019.

164. FALCONER, H. Notes on fossil species of *Cervus*, including a description of a remarkable fossil antler of a large species of extinct *Cervus*, *C.* (*Eucladoceros*) *Sedgwickii*, in the collection of the Rev John Gunn, Irstead. In: MURCHISON, C., ed., *Palaeontological Memoirs and Notes of Hugh Falconer, Vol. II. Mastodont, elephant, rhinoceros, ossiferous caves, primeval man and his* contemporaries, London: Robert Hardwicke, 1868, pp. 471-480.

165. FARRIS, JS. On the cophenetic correlation coefficient. *Systematic Zoology*, 1969, nr. 18, pp. 279-285.

166. FEJFAR, O., HEINRICH, WD., HEINTZ, E.. Neues aus dem Villafranchium von Hajnácka bei Filakovo (Slowakei, CSSR). *Quatärpaläontologie,* 1990, nr. 8, pp. 47-70. ISSN 0138-3116.

167. FERNANDEZ, P., BOUZOUGGAR, A., COLLINA-GIRARD, J., COULON, M. The last occurrence of *Megaceroides algericus* Lydekker, 1890 (Mammalia, Cervidae) during the middle Holocene in the cave of Bizmoune (Morocco, Essaouria region). *Quaternary International*, 2015, nr. 374, pp. 154-167. ISSN 1040-6182.

168. FISCHER, G. *Bibliographia Palaeontologica Animalium Systematica*. Moscow: Typis Universitatis Caesareae, 1834. 414 p.

169. FISCHER, G. Notice sur les fossiles et les pétrifications du gouvernement de Moscou. *Bulletin de la Société Impériale des naturalistes de Moscou*, 1838. nr. 5, pp. 530-543.

170. FLEROV, KK. A new Paleolithic reindeer from Siberia. *Journal of Mammology*, 1934, nr. 15(3), pp. 239-240.

171. FLEROV, KK. Morphology and ecology of deer and the process of their evolution. *Materials on the Quaternary Period of the USSR*, 1950, nr. 2, pp. 50-69 (in Russian).

172. FLEROV, KK. Musk deer and deer. In: Novikov, GA., ed*.* *The Fauna of USSR. Mammals 1(2)*, Moscow-Leningrad: Academy of Sciences of USSR, 1952, 256 p. (in Russian).

173. FLEROV, KK. Family Cervidae Gray 1821. In: Gromova, VI., ed. *Basics of paleontology, 13. Mammals*. Moscow: Nedra, 1962, pp. 368-378 (in Russian).

174. FOSTER, JB. Evolution of mammals on islands. *Nature*, 1964, nr. 202(4929), pp. 234-235.

175. FRANZMANN, AW. *Alces alces*. *Mammalian Species*, 1981, nr. 154, pp. 1-7. ISSN 1545-1410.

176. FRICK, C. Horned ruminants of North America. *Bulletin of the American Museum of Natural History*, 1937, nr. 69, pp. 1-669.

177. GAMBARIAN, PP. *The running of mammals: adaptational features of locomotional organs*. Leningrad: Nauka, 1972, 334 p. (in Russian).

178. GASTALDI, B. Genni sulla giacitura del *Cervus Euryceros*. *Atti dei Lincei, Roma, Ser. II*, 1875, nr. 2, pp. 436-441.

179. GAUDRY, A. *Animaux fossiles et géologie de l'Attique*. Paris: F. Savy, 1862, 475 p.

180. GAUDRY, A. *Animaux fossiles et géologie de l'Attique - Atlas*. Paris: F. Savy, 1867, 95 p.

181. GEIST, V. The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the Old World deer and the genus *Bison*. *Quaternary Research*, 1971, nr. 1(3), pp. 285-315.

182. GEIST, V. *Deer of the World: Their Evolution, Behaviour, and Ecology*. Mechanicsburg (PA): Stackpole Books, 1998, 421 p. ISBN: 0811704963, 9780811704960.

183. GENTRY, A. Case 2928. Regnum Animale..., Ed. 2 (MJ Brisson, 1762): proposed rejection, with the conservation of the mammalian generic names *Philander* (Marsupialia), *Pteropus* (Chiroptera), *Glis*, *Cuniculus* and *Hydrochoerus* (Rodentia), *Meles*, *Lutra* and

Hyaena (Carnivora), *Tapirus* (Perissodactyla), *Tragulus* and *Giraffa* (Artiodactyla). *Bulletin of Zoological Nomenclature*, 1994, nr. 51 (2), pp. 135-146. ISSN:0007-5167

184. GENTRY, AW. Ruminants of Rudabanya. *Palaeontographia Italica*, 2005, nr. 90, pp. 283-302. ISSN 0373-0972.

185. GENTRY, AW. Cervidae. In: Werdelin L. and Sanders W. J. (Eds.): Cenozoic mammals of Africa. Berkeley (CA): University of California Press, 2010. pp. 813-814. ISBN 9780520257214.

186. GENTRY, AW., RÖSSNER GE., HEIZMANN EPJ. Suborder Ruminantia. In: Rössner, GE., Heissig, K., eds. The Miocene Land Mammals of Europe. München : Verlag Dr. Friedrich Pfeil, 1999: pp. 225-258,. ISBN 9783931516505.

187. GERVAIS, P. *Zoologie et paleontologie francaises. Nouvelles recherches sur les animaux vertebres*. Deuxieme edition. Paris: Arthus Bertrand, 1859, 544 p. + Atlas, 95 p.

188. GESSNER, C. *Historia animalium. I. Quadrupedibus viviparis*. Zurich, 1551, 1104 p.

189. GIBBARD, PL., HEAD, MJ. IUGS ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Quaternaire*, 2009, nr. 20(4), pp. 411-412. ISSN 1142-2904.

190. GIBBARD, PL., HEAD, MJ., WALKER, MJ. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science*, 2010, nr. 25(2), pp. 96-102. ISSN 0267-8179.

191. GILBERT, C., ROPIQUET, A., HASSANIN, A. Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): Systematics, morphology, and biogeography. *Molecular Phylogenetics and Evolution*, 2006, nr. 40, pp. 101-117. ISSN 1055-7903.

192. GLIOZZI, E., ABBAZZI, L., ARGENTI, A., AZAROLI, A., CALOI, L., CAPASSO BARBATO, L., DI STEFANO, G., ESU, D., FICCARELLI, G., GIROTTI, O., KOTSAKIS, T., MASINI, F., MAZZA, P., MEZZABOTTA, C., PALOMBO, M. R., PETRONIO, C., ROOK, L., SALA, B., SARDELLA, R., ZANALDA, E., TORRE, D.. Biochronology of selected Mammals, Molluscs and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 1997, nr. 103(3), pp. 369-388. ISSN 0035-6883.

193. GLIOZZI, E., MALATESTA, A. A Megacerine in the Pleistocene of Sicily. *Geologica Romana*, 1982, nr. 21, pp. 113-395. ISSN 0435-3927.

194. GLIOZZI, E., MALATESTA, A., SCALONE, E. Revision of *Cervus elaphus siciliae* Pohlig, 1893, Late Pleistocene endemic deer of the Siculo-Maltese district. *Geologica Romana*, 1993, nr. 29, pp. 307-353. ISSN 0435-3927.

195. GODINA, AY., GROMOVA, VI., SOKOLOV, II., TROFIMOV, BA., FLEROV, KK., HAVESON, YI. Order Artiodactyla, even-toed ungulates. In: Gromova, VI. (Ed), Basics of Palaeontology: Mammals. Moscow: Nedra, 1962, pp. 337-341 (in Russian).

196. GRAY, JE. On the Natural Arragement of Vetrebrose Animals. *The London Medical Repository*, 1821, nr. 15, pp. 296-310.

197. GROMOV, VI. Paleontological and Archeological Fundamentals of the Continental Deposits of the Quaternary Period. *Transactions of the Geological Institute*, 1948, nr. 64(17), pp. 1-521 (in Russian).

198. GROSSOUVRE, DE A., STEHLIN, HG. Les sables de Rosières, près Saint-Florent (Cher). *Bulletin de la Société géologique de France*, 1912, nr. 12, pp.194-212.

199. GROVES, CP. The genus *Cervus* in eastern Eurasia. European Journal of Wildlife Research, 2005, nr. 52(1), pp. 14-22. ISSN 1612-4642.

200. GROVES, CP. Current taxonomy and diversity of crown ruminants above the species level. *Zitteliana*, *Series B*, 2013, nr. 31, pp. 12-13. ISSN 1612-4138.

201. GROVES, CP., GRUBB, P. Relationships of living deer. In: CM Wemmer (Ed.), *Biology and Management of the Cervidae*. Washington: Smithsonian Institution Press, 1987, pp. 21-59. ISBN 9780874749816.

202. GROVES, CP., GRUBB, P. Muntiacidae. In: G Bubenik and A Bubenik (Eds.), *Horns, prong-horns, and antlers*. New-York: Springer-Verlag, 1990, pp. 134-168. ISBN 3540971769.

203. GROVES, CP., GRUBB, P. *Ungulate taxonomy*. Baltimore, MD: Johns Hopkins University Pres, 2011. 317 p. ISBN 9781421400938.

204. GRUBB, P. Valid and invalid nomenclature of living and fossil deer. *Acta Theriologica*, 2000, nr. 45(3), pp. 289-307. ISSN 0001-7051.

205. GUERIN, C., YVETTE DEWOLF, Y., LAUTRIDOU, JP. Révision d'un site paléontologique célèbre : Saint-Prest (Chartres, France). *Geobios*, 2003, nr. 36, pp. 55-82. ISSN 0251-1223.

206. HADJOUIS, J. *Megaceroides algericus* (Lydekker, 1890), du gisement des Phacochères (Alger, Algérie). Etude critique de la position systematique de *Megaceroides*. *Quaternaire*, 1990, nr. 3-4, pp. 247-258. ISSN 1142-2904.

207. HAMMER, Ø., HARPER, DAT., RYAN, PD. PAST - palaeontological statistics software package for education and data analysis. *Palaeonologia Electronica*, 2001, nr. 4(1), pp. 9. ISSN 1094-8074.

208. HARMER, SF. On a specimen of *Cervus belgrandi* Lart. (*C. verticornis* Dawk.) from the Forest Bed of East Anglia. *Transactions of Zoological Society of London*, 1899, nr. 15, pp. 25-35.

209. HART, BL. Effects of hormones on behavioral defenses against parasites. In: Beckage NE (Ed.): *Parasites and Pathogens: Effects on Host Hormones and Behavior*. Boston: Springer, 1997. pp. 210-230. ISBN 9780412074011.

210. HART, J. *Description of the Skeleton of the Fossil Deer of Ireland, (*Cervus megaceros*), in the Museum of the Royal Dublin Society*. Dublin: R. Grainsberry, 1825. 31 p.

211. HASSANIN, A., DELSUC, F., ROPIQUET, A., HAMMER, C., VAN VUUREN, B. J., MATTHEE, C., RUIZ-GARCIA, M., CATZEFLIS, F., ARESKOUG, V., NGUYEN, T. T., COULOUX, A. Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies*, 2012, nr. 335, pp. 32-50. ISSN 1631-0691.

212. HAUG, GH., TIEDEMANN, R. Effect of the formation of the Isthmus of Panama on Atlantic Ocean thermohaline circulation. *Nature*, 1998, nr. 393(6686), pp. 673-676. ISSN 0028-0836.

213. HEINTZ, E. Les cervidés villafranchiens de France et d'Espagne. *Mémoires du Muséum national d'histoire naturelle. Série C, Sciences de la terre,* 1970, nr. 22(1), pp. 1-303, Figures et tableaux (2), pp. 1-206. ISSN 1243-4442.

214. HEINTZ, E., POPLIN, F. *Alces carnutorum* (Laugel, 1862) du Pléistocéne de Saint-Prest (France) : Systematique et évolution des Alcinés (Cervidae, Mammalia). *Quartärpaläontologie*, 1980, nr. 4, pp. 106-122. ISSN 0138-3116.

215. HEPTNER, VG., ZALKIN, VI. Deer of the USSR. *Transactions on Study of Fauna and Flora of the USSR*, 1947, nr. 10(25), pp. 1-176 (in Russian).

216. HERNANDEZ FERNANDEZ, M., ALBERDI, M.T., AZANZA, B., MONTOYA, P., MORALES, J., NIETO, M., PELAEZ-CAMPOMANES, P. Identification problems of arid environments in the Neogene-Quaternary mammal record of Spain. *Journal of Arid Environments*, 2006, nr. 66, pp. 585-608. ISSN 0140-1963.

217. HIBBARD, CW. The Occurrence of *Cervalces scotti* Lydekker in Kansas. *Transactions of Kansas Academy of Sciences*, 1940, nr. 43, pp. 411-415.

218. HIBBERT, S. Additional Contributions towards the History of the *Cervus euryceros*, or Fossil Elk of Ireland. *Edinburgh journal of science*, 1825, nr. 2(2), pp. 301-317.

219. HIGHAM, T., COMPTON, T., STRINGER, C., JACOBI, R., SHAPIRO, B., TRINKAUS, E., CHANDLER, B., GRÖNING, F., COLLINS, C., HILLSON, S., O'HIGGINS, P. The earliest evidence for anatomically modern humans in northwestern Europe. *Nature*, 2011, nr. 479(7374), pp. 521-524. ISSN 0028-0836.

220. HILZHEIMER, M. Uber die Systematic einiger fossiler Cerviden. *Centralblatt für Mineralogie, Geologie und Paläontologie*, 1922, nr. 18. pp. 741-749.

221. HODGSON, BH. Proceedings of Learned Societies. Linnaean Society, Feb. 20, 1838. *Annales of Natural History*, 1838, nr. 1, pp. 152-154.

222. HODGSON, BH. Specific name and character of a new species of *Cervus*, discovered by B. H. Hodgson, Esq. in 1825, and indicated in his Catalogue by the local name of Bahraiya. *The Journal of the Asiatic Society of Bengal*, 1835, nr. 4, pp. 648-649.

223. HUGHES, S., HAYDEN, Th. J., DOUADY, C. J., TOUGARD, C., GERMONPRÉ, M., STUART, A., LBOVA, L., CARDEN, R. F., HÄNNI, K., SAY, L. Molecular phylogeny of the extinct giant deer, *Megaloceros giganteus*. *Molecular Phylogenetics and Evolution*, 2006, nr. 40, pp. 285-291. ISSN 1095-9513, 1055-7903.

224. ICZN, International Code of Zoological Nomenclature, 2012. RIDE, WDL., COGGER. HG., DUPUIS, C., KRAUS, O., MINELLI, A., THOMPSON, FC., TUBBS, PK.. eds. [Citat: 22.11.2022] ISBN: 0-85301-006-4. Disponibil: https://www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/the-code-online/.

225. JANIS, CM. Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: DAMUTH, J., MACFADDEN, BJ., eds. *Body size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge: Cambridge University Press, 1990, pp. 255-299. ISBN 9780521019330.

226. JANIS, CM., EHRHARDT, D. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, 1988, nr. 92(3), pp.267-284. ISSN 0024-4082.

227. JANIS, CM., LISTER, A. The morphology of the lower fourth premolar as a taxonomic character in the ruminania (Mammalia, Artiodactyla), and the systematic position of *Triceromeryx*. *Journal of Paleontology*, 1985, nr. 59(2), pp. 405-410. ISSN 0022-3360.

228. JANIS, CM., SCOTT, KM. The Interrelationships of Higher Ruminant Families with Special Emphasis on the Members of the Cervoidea. *American Museum Novitates*, 1987, nr. 2893, pp. 1-85, New-York. ISSN 0003-0082.

229. JANOVSKAYA, NM. New deer from middle Pliocene of Moldavia. *Transactions of the Palaeontological Institute*, 1954, nr. 47, pp. 163-171 (in Russian).

230. JOHNSON, R. Notice of a New Species of Deer from the Norfolk Forest-Bed. *The Annals and Magazine of Natural History, ser. 4*, 1874, nr. 13(73), pp. 1-4.

231. JOLEAUD, L. Sur le *Cervus* (*Megaceroides*) *algericus* Lydekker, 1890. *Comptes rendus des séances de la Société de biologie et de ses filiales*, 1914, nr. 76, pp. 737-739.

232. JOLEAUD, L. *Cervus* (*Megaceroides*) *algericus* Leydekker, 1890. *Recueil des Notices et Mémoires de la Société Archéologique du Département de Constantine*, 1916, nr. 49, pp. 1-67.

233. JONSTON, J. *Historiae naturalis de quadrupedibus libri: cum aeneis figuris*. Francofurti ad Moenum: Impensis haeredum Math. Meriani, 1652. 232 p.

234. KAHLKE, HD.. *Die Cervidenreste aus den Altpleistozanen Ilmkiesen von Süßenborn bei Weimar*. Berlin: Akademie Verlag, 1956. 62 p.

235. KAHLKE, HD. *Rangifer* aus den Sanden von Mosbach. *Paläontologische Zeitschrift*, 1963, nr. 37(3), pp. 277-282.

236. KAHLKE, HD. Die Cerviden-Reste aus dem Tonen von Voigtstedt in Thüringen. *Paläontologische Abhandlungen. Abteilung A*, 1965, nr. 2 (2/3), pp. 381-431.

237. KAHLKE, HD.. Die Cerviden-Reste aus den Kiesen von Süßenborn bei Weimar. *Palaeontologische Abhandlungen. Abteilung A, Palaozoologie*, 1969, nr. 3(3-4), pp. 367-788.

238. KAHLKE, H.-D., 1971. Family Cervidae Gray, 1821. In: Nikiforova, K. V. (Chief Ed.), Pleistocene of Tiraspol, Chișinău: Știința, pp. 137-156 (in Russian).

239. KAHLKE, HD. Die Cerviden-reste aus dem Unterpleistozän von Untermassfeld. Das Pleistozän von Untermassfeld bei Meningen (Thüringen), Teil 1. *Monographien des Römisch-Germanischen Zentralmuseums Mainz*, 1997, nr. 40(1), pp. 181-275. ISSN 0171-1474.

240. KAHLKE, HD. Neufunde fon Cerviden-resten aus dem Unterpleistozän von Untermassfeld. Das Pleistozän von Untermassfeld bei Meningen (Thüringen), Teil 2. *Monographien des Römisch-Germanischen Zentralmuseums Mainz*, 2001, nr. 40(2), pp. 461-482. ISSN 0171-1474.

241. KAHLKE, RD. *The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus-Coelodonta Faunal Complex in Eurasia (Large Mammals)*. Rapid City: Fenske Companies, 1999. 219 p.

242. KELLY, J. An Account of the Strata met with in digging for Marle, and of Horns found under Ground in Ireland. *Philosophical Transactions*, 1727, nr. 34(394), pp. 122-123.

243. KHOMENKO, I. Meotian fauna of v. Tarakliya of Bendery district. 1. The ancestors of modern and fossil Cervinae. 2. Giraffidae and Cavicornia. *Annuaire géologique et minéralogique de la Russie*, 1913, nr. 15, pp. 107–132 (in Russian).

244. KHOMENKO, I. L'etage Roussillionien dans le Pliocene moyen de la Bessarabie et son importance pour determiner l'age des sables de Balta et des depôts de Kouyalnik. *Travaux de la Société des naturalistes et des amateurs des sciences naturelles*, 1917, nr. 6, pp. 50-75.

245. KITCHENER, A. Fighting behaviour of the extinct Irish elk. *Modem Geology*, 1987, nr. 11, pp. 1-28. ISSN 0026-7775.

246. KNOWLTON, T. An Account of Two extraordinary Deers Horns, found wider-ground in different Parts of Yorkfhire. *Plilosophical Transactions*, 1746, nr. 44(479), pp. 124-127.

247. KÖHLER, M. Skeleton and Habitat of recent and fossil Ruminants. *Münchner Geowissenschaftliche Abhandlungen (A)*, 1993, nr. 25, pp. 1-88. ISSN 0177-0950.

248. KOLFSCHOTEN, T. VAN, VAN DER JAGT, I., BEEREN, Z., ARGITI, V., VAN DER LEIJE, J., VAN ESSEN, H., BUSSCHERS, F. S., STOEL, P., VAN DER PLICHT, H.. A remarkable collection of Late Pleistocene reindeer (*Rangifer tarandus*) remains from Woerden (The Netherlands). *Quaternary International*, 2011, nr. 238, pp. 4-11. ISSN 1040-6182.

249. KOROTKEVICH, EL. New data on the taxonomy and phylogeny of the genus *Procapreolus*. *Dopovidi Akademii Nauk Ukrainskoi RSR*, 1963, nr. 10, pp. 1390-1393 (in Ukrainian).

250. KOROTKEVICH, EL. New Finds of Pliocene Roe-Deer of the Genus *Procapreolus* in the South of the USSR. *Dopovidi Akademiy Nauk Ukraynskoy RSR*, 1964a, nr. 3, pp. 382-386 (in Ukrainian).

251. KOROTKEVICH, EL. A new species of fossil *Muntiacus* from the Pliocene deposits of the south of USSR. *Dopovidi Akademii Nauk Ukraynskoy RSR*, 1964b, nr. 6: pp. 807-809 (in Ukrainian).

252. KOROTKEVICH, EL. A new roe deer species from the Maeotis of the Ukraine. *Paleontological Journal*, 1965a, 4: 60-67 (in Russian).

253. KOROTKEVICH, EL. On deer from Pliocene of Kuchurgan and their paleobiogeographical significance. *Prirodnaja obstanovka i fauny proshlogo*, 1965b, nr. 2, pp. 25-43 (in Russian).

254. KOROTKEVICH, EL. *Late Neogene Deer of the North Blak Sea Area*. Kiev: Naukova Dumka, 1970. 175 p. (in Russian).

255. KOROTKEVICH, EL. New representative of the genus *Procapreolus* from the territory of the North Black Sea Area. *Vestnik zoologii*, 1974, nr. 6, pp. 68-77 (in Russian).

256. KOROTKEVICH, EL. *The history of development of the* Hipparion *fauna from Eastern Europe*. Kiev, Naukova Dumka, 1988, 160 p. (in Russian). ISBN 5-12-000281-1.

257. KOSTOPOULOS, DS. The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece 9. Cervidae and Bovidae. *Palaeontographica Abteilung A*, 2006, nr. 276, pp.151-183. ISSN 0375-0442.

258. KOSTOPOULOS, DS. The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia - 1. The fossiliferous site "Apollonia-1", Mygdonia basin of Greece. *Geodiversitas*, 1997, nr. 19(4), pp. 845-875. ISSN 1280-9659.

259. KOSTOPOULOS, DS., ATHANASSIOU, A. In the shadow of bovids: suids, cervids and giraffids from the Plio-Pleistocene of Greece. *Quaternaire Hors-série*, 2005, nr. 2, pp. 179-190. ISSN 1771-1150.

260. KRIJGSMAN, W., TESAKOV, A., YANINA, T., LAZAREV, S., DANUKALOVA, G., VAN BAAK, C.G., AGUSTÍ, J., ALÇIÇEK, M.C., ALIYEVA, E., BISTA, D., BRUCH, A. Quaternary time scales for the Pontocaspian domain: Interbasinal connectivity and faunal evolution. *Earth-science reviews*, 2019, nr. 188, pp. 1-40. ISSN 0012-8252.

261. KUSS, E. Die pleistozänen Hirsche der ostmediterranen Inseln Kreta, Kasos, Karpathos und Rhodos (Griechenland). *Berichte der naturforschenden Gesellschaft zu Freiburg im Breisgau*, 1975, nr. 65, pp. 25-79.

262. KURTEN, B. *Pleistocene Mammals of Europe*. Chicago: Aldine Publ. Co., 1968. 317 p.

263. KUWAYAMA, R, OZAWA, T. Phylogenetic Relationships among European Red Deer, Wapiti, and Sika Deer Inferred from Mitochondrial DNA Sequences. *Molecular Phylogenetics and Evolution*, 2000, 15 (1): 115-123. ISSN 1055-7903.

264. KYNKÄÄNNIEMI, S.M., KETTU, M., KORTET, R., HÄRKÖNEN, L., KAITALA, A., PAAKKONEN, T., MUSTONEN, A. M., NIEMINEN, P., HÄRKÖNEN, S., YLÖNEN, H., LAAKSONEN, S. Acute impacts of the deer ked (*Lipoptena cervi*) infestation on reindeer (*Rangifer tarandus tarandus*) behavior. *Parasitology research*, 2014, nr. 113(4), pp. 1489-1497. ISSN 0932-0113.

265. LALUEZA-FOX, C., BERTRANPETIT, J., ALCOVER, JA., SHAILER, N., HAGELBERG, E. Mitochondrial DNA from *Myotragus balearicus*, an extinct bovid from the Balearic Islands. *Journal of Experimental Zoology*, 2000, nr. 288(1), pp. 56-62. ISSN 2471-5646.

266. LAQUAY, G. *Cervus elaphus* (Mammalia, Artiodactyla) du Pleistocene superieur de la Carriere Doukkala II (Rabat – Maroc). Sa comparaison avec le cerf Wurmien de France. *Revue de Paleobiologie*, 1986, nr. 5(1), pp. 143-147. ISSN 0253-6730.

267. LAUGEL, L. La faune de Saint-Prest près de Chartres (Eure et Loir). *Société géologique de France*, 1862, 10 p.

268. LEONARDI, G., PETRONIO, C. I Cervi Pleistocenici del bacino diatomitico di Riano (Roma). *Atti della Academia nazionale dei Lincei, Classe di Scienze fiziche, matematiche e naturali – serie VIII*, 1974, nr. 12(3), pp. 103-208.

269. LEONARDI, G, PETRONIO, C. The fallow deer of the European Pleistocene. *Geologica Romana*, 1976, nr. 15, pp. 1-67. ISSN 0435-3927.

270. LINNAEUS, C. *Systema Naturae. Editio duodecima, reformata. Tomus I: Impensis Direct*. Stockholm: Laurentii Salvii, 1766. 532 p.

271. LISTER, A. Diversity and Evolution of Antler Form in Quaternary Deer. In: Wemmer, CM., ed. *Biology and Management of Cervidae*. Washington: Smithsonian, 1987, pp. 81-98. ISBN 978-0874749816.

272. LISTER, A. Critical reappraisal of the middle Pleistocene deer "*Cervus*" *elaphoides* Kahlke. *Quaternaire*, 1990, nr. 3-4, pp. 175-192. ISSN 11422904.

273. LISTER, A. The stratigraphical significance of deer species in the Cromer Forest-bed Formation. *Journal of Quaternary Science*, 1993, nr. 8(2), pp. 95-108. ISSN 0267-8179.

274. LISTER, A. The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zoological Journal of the Linnean Society*, 1994, nr. 112, pp. 65-100. ISSN 0024-4082.

275. LISTER, A. The Pliocene deer of the Red Crag Nodule Bed (UK). *Deinsea*, 1999, nr. 7, pp. 215-221. ISSN 0923-9308.

276. LISTER, A., CHAPMAN, NG. Variation in lateral metacarpals of fallow deer, *Dama dama* (Mammalia, Cervidae). *Journal of Zoology*, 1988, nr. 216, pp. 597-603. ISSN 0952-8369.

277. LISTER, A., EDWARDS, CJ., NOCK, DAW., BUNCE, M., VAN PIJLEN, IA., BRADLEY, DG., THOMAS, MG., BARNES, I. The phylogenetic position of the "giant deer", *Megaloceros giganteus*. *Nature*, 2005, nr. 348(8), pp. 850–853. ISSN 0028-0836.

278. LISTER A., GRUBB P., SUMNER SRM. 1998. Taxonomy, morphology and evolution of European roe deer. In: ANDERSEN, R., DUNCAN, P., LINNELL, JDC. eds. *The European Roe Deer: The Biology of Success*. Oslo: Scandinavian University Press, pp. 23-46. ISBN 8200376826.

279. LÖNNBERG, E. Which is the taxonomic position of the Irish Giant Deer and allied races? *Arkiv för Zoologie*, 1906, nr. 3(14), pp. 1-8.

280. LÖNNBERG, E. Taxonomic Notes about Palearctic Reindeer. *Arkiv für Zoologie*, 1909, nr. 6(4), pp. 1-18.

281. LUDT, C., SCHROEDER, W., ROTTMANN, O., KUEHN, R.. Mitochondrial DNA phylogeography of red deer (*Cervus elaphus*). *Molecular Phylogenetics and Evolution*, 2004, nr. 31, pp. 1064-1083. ISSN 1055-7903.

282. LUNGU, A., RZEBIK-KOWALSKA, B. *Faunal assemblages, stratigraphy and taphonomy of the Late Miocene localities in the Republic of Moldova*. Kraków: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, 2011. 62 p. ISBN 8361358404.

283. LYDEKKER, R. *Catalogue of the fossil Mammalia in the British Museum (Natural History). Part II. The Order Ungulata, Suborder Artiodactyla*. London: British Museum (Natural History), 1885, 324 p.

284. LYDEKKER, R. On a cervine jaw from Algeria. *Proceedings of Zoological Society*, 1890, nr. 1890, pp. 602-604.

285. LYDEKKER, R. *Deer of all lands: A history of the family cervidae living and extinct*. London: Rowland Ward, Ltd., 1898, 329 p.

286. LYDEKKER, R. *Catalogue of the Ungulate Mammals in the British Museum (Natural History). Vol. IV. Artiodactyla, Families Cervidae (Deer), Tragulidae (Chevrotains), Camelidae (Camels and Llamas), Suidae (Pigs and Peccaries), and Hippopotamidae (Hippopotamuses)*. London: British Museum (Natural History), 1915. pp. 1-438.

287. MA, S., WANG, Y. XU, L. Taxonomic and Phylogenetic Studies of the Genus *Muntiacus*. *Acta Theriologica Sinica*, 1986, nr. 6(3), pp. 190-209. ISSN 10001050.

288. MACAROVICI, N. Contribution à la connaissance d'*Alces palmatus* Ham. Smith dans le Quaternaire de la Roumanie. *Eiszeitalter und Gegenwart*, 1962, nr. 12(1), pp. 66-72.

289. MAIN, AJ., SPRANCE, HE., KLOTER, KO., BROWN, SE. *Ixodes dammini* (Acari: Ixodidae) on white-tailed deer *Odocoileus virginianus* in Connecticut, USA. *Journal of Medical Entomology*, 1981, nr. 18, pp. 487-492. ISSN 0022-2585.

290. MARKOV, GG., DANILKIN, AA. Geographic craniometrics variability and intraspecific taxonomy of the red deer (*Cervus elaphus* L.) in Palearctic. In: ZOMBORSZKY, Z., ed. *Advances in Deer Biology: Proceedings of the 4th International Deer Biology Congress, 30 June - 4 July, 1998, Kaposvár: Hungary*, 1999. pp. 119-120. ISBN 9789639096530, 9639096539.

291. MARTINEZ-NAVARRO B., TORO I., AGUSTI J. Las asociaciones de grandes mamíferos de Fuente Nueva-3 y Barranco León-5 (Orce, Granada, España): resultados preliminares. In: BAQUEDANO E., RUBIO JARA S., eds. *Zona Arqueológica, Miscelánea en homenaje a Emiliano Aguirre. Paleontología, Museo Arqueológico Regional, Comunidad de Madrid Alcalá de Henares*, 2004, nr. 4, pp. 293-305. ISSN 1579-7384.

292. MEIJAARD E., GROVES CP. Morphometrical relationships between South-east Asian deer (Cervidae, tribe Cervini): Evolutionary and biogeographic implications. *Journal of Zoology*, 2004, nr. 263(2), pp. 179-196. ISSN 0952-8369.

293. MEIN, P. Updating of MN Zones. In: LINDSAY EH., FAHLBUSCH V., MEIN P., eds. *European Neogene Mammal Chronology. NATO ASI Series – Series A: Life Sciences*, 1989, nr. 180, pp. 73-90. ISBN 978-1-4899-2515-2.

294. MEIRI M., LISTER AM., HIGHAM TFG., STEWART JR., STRAUS LG., OBERMAIER H., GONZALES MORALES MR., MARIN-ARROYO AB., BARNES I.. Late-glacial recolonization and phylogeography of European red deer. *Molecular Ecology*, 2013, nr. 2013, pp. 1-12. ISSN 0962-1083.

295. MELENTIS JK. Studien uber Fossile Vertebraten Griechenlands. 20. *Orthogonoceros verticornis* aus dem Altpleistozän des Beckens von Haliakmon (Griechenland). *Proceedings of the Athens Academy*, 1967, nr. 42, pp. 79-88.

296. MELENTIS JK. Zur Morphologie und systematischen Stellung von *Pliocervus pentelici* (Gaudry) aus dem Pont von Attika. *Proceedings of the Athens Academy*, 1968, nr. 43, pp. 6-16.

297. MELIS RT., PALOMBO MR., GHALEB B., MELONI S. A key site for inferring the timing of dispersal of giant deer in Sardinia, the Su Fossu de Cannas cave, Sadali, Italy. *Quaternary Research*, 2016, nr. 86(3), pp. 335-347. ISSN 0033-5894.

298. MENÉNDEZ E. Cérvidos del yasimiento del Pleistoceno inferior de Venta Micena-2, Orce (Granada, Espaňa). *Paleontologia i Evolució*, 1987, nr. 1, pp. 129-181. ISSN 0211-609X.

299. MENNECART B., DEMIGUEL D., BIBI F., RÖSSNER GE., METAIS G., NEENAN JM., WANG S., SCHULZ G., MÜLLER B., COSTEUR L.. Bony labyrinth morphology clarifes the origin and evolution of deer. *Scientific Reports*, 2017, nr. 7, nr. 13176, 11 p., doi:10.1038/s41598-017-12848-9. ISSN 2045-2322.

300. MIYAMOTO M., KRAUS F., RYDER OA. Phylogeny and evolution of antlered deer determined from mitochondrial DNA sequences. *Proceedings of National Academy of Sciences of United States of America*, 1990, nr. 87, pp. 6127-6131. ISSN 0027-8424.

301. MOLYNEUX, Th. A Discourse Concerning the Large Horns Frequently Found under Ground in Ireland, Concluding from Them That the Great American Deer, Call'd a Moose, Was Formerly Common in That Island: With Remarks on Some Other Things Natural to That Country. *Philosophical Transactions of the Royal Society*, 1697, nr. 19, pp. 489-512.

302. MOORING, MS., BLUMSTEIN, DT., STONER, CJ. The evolution of parasite-defense grooming in ungulates. *Biological Journal of the Linnean Society*, 2004, nr. 81(1), pp. 17-37. ISSN: 0024-4066.

303. MOORING, MS., SAMUEL, WM. Tick-removal grooming by elk (*Cervus elaphus*): testing the principles of the programmed-grooming hypothesis. *Canadian Journal of Zoology*, 1998, nr. 76(4), pp. 740-750. ISSN 0008-4301.

304. MORALES, J., PICKFORD, M., SORIA, D. Pachyostosis in a Lower Miocene giraffoid from Spain, *Lorancameryx pachyostoticus* nov. gen. nov. sp. and its bearing on the evolution of bony appendages in artiodactyls. *Geobios*, 1992, nr. 26(2), pp. 207-230. ISSN 0016-6995.

305. MOSBRUGGER, V. Climate change and water cycle-some lessons from the geological past. In: ZEREINI, F., HÖTZL, H., Eds.; *Climatic changes and water resources*

in the Middle East and North Africa. Berlin-Heidelberg: Springer, 2008; pp. 3-13. ISBN 978-3-540-85047-2.

306. MOULLADE, E. Note sur une nouvelle espece de daim fossile. *Mémoires de la Société d'agriculture et sciences d'Haute Loire*, 1886, nr. 4, pp. 304-306.

307. MOULLÉ PE., LACOMBAT F., ECHASSOUX A. Contribution of the large mammals of Vallonnet cave (Roquebrune-Cap-Martin, Alpes-Maritimes, France) to the knowledge of biochronological frame of the second half of the Lower Pleistocene in Europe. *L'Anthropologie*, 2006, nr. 110, pp. 837-849. ISSN 0003-5521.

308. MYSTKOWSKA ET. Morphological variability of the skull and body weight of the red deer. *Acta theriologica* 1966, 11(5-9), pp. 129-194.

309. NEHRING A. Über eine besondere Riesenhirsche-Rasse aus der Gegen von Kottbus. *Sitzungs-Bericht Gesellscliatt uaturtbrschencler Freunde*, 1891, nr. 8, pp. 151–162.

310. NEWTON, ET. The Vertebrata of the Forest Bed Series of Norfolk and Suffolk. *Memoires Geologocal Survey of England and Wales*, 1882, 143 p.

311. NEWTON, ET. *The Vertebrata of the Pliocene deposits of Britain*. London: HM Stationery Office, 1891.216 p.

312. NIKOLSKY PA. *Systematics and stratigraphical significance of elks (Alcini, Cervidae, Mammalia) in Late Caenozoic of Eurasia and Northern America*. Author's abstract of dissertation, Moscow, 2010. 26 p.

313. NIKOLSKY PA., BOESKOROV GG. Primitive and derived features in the teeth of modern moose (*Alces*, Cervidae, Mammalia) from Eastern Siberia. *Russian Journal of Theriology*, 2011, nr. 10(1), pp. 27-30. ISSN 1682-3559.

314. NIKOLSKY PA., TITOV VV. 2002. *Libralces gallicus* (Cervidae, Mammalia) from the Upper Pliocene of the Northeast Azov Region. *Paleontological Journal*, 36(1), pp. 87-93. ISSN 0031-0301.

315. O'DEA A., LESSIOS HA., COATES AG., EYTAN RI., RESTREPO-MORENO SA., CIONE AL., COLLINS LS., DE QUEIROZ A., FARRIS DW., NORRIS RD., STALLARD RF. Formation of the Isthmus of Panama. *Science advances*, 2016, nr. 2(8), p.e1600883. ISSN 2375-2548.

316. OWEN, R. Report on the British Fossil Mammalia. Part II. Ungulata. In: *Report of the Thirteenth Meeting of the British Association for the Advancement of Science held at Cork in August 1843*, London: John Murray, 1844. pp. 208-241.

317. OWEN, R. *A History of British Fossil Mammals and Birds*. London: John van Voorst, 1846. 560 p.

318. PALOMBO, MR. I grandi mammiferi pleistocenici delle isole del Mediterraneo: tempi e vie di migrazione. *Bollettino della Società Paleontologica Italiana*, 1986, nr. 24(2-3), pp. 201-224. ISSN 03757633.

319. PARFITT SA., LISTER AM. The Ungulates from the Peştera cu Oase. In: TRINKAUS E., CONSTANTIN S., ZILHAO J., eds. *Life and Death at the Peştera cu Oase: A Setting for Modern Human Emergence in Europe*. Oxford: Oxford University Press, 2013, pp.189-203. ISBN 9780195398229.

320. PENNANT, T. *Synopsis of Quadrupeds*. Chester: J. Monk, 1771. 382 p.

321. PEREIRA, E. *Cervus elaphus rossii* (Mammalia, Artiodactyla), a new endemic subspecies from the Middle Pleistocene in Corsica. *Palaeovertebrata*, 2001, nr. 30(2-4), pp. 189-213. ISSN 0031-0247.

322. PETRIE, M. Intraspecific variation in structures that display competitive ability: large animals invest relatively more. *Animal Behaviour*, 1988, nr. 36(4), pp. 1174-1179. ISSN 0003-3472

323. PETRONIO, C. *Dama nestii eurygonos* Azz. di Capena (Roma). *Geologica Romana*, 1979, nr. 18, pp. 105-125. ISSN 0435-3927.

324. PETRONIO, C. Les cervidés endémiques des îles méditerranéennes. *Quaternaire*, 1990, nr. 3-4, pp. 259-264. ISSN 1965-0795.

325. PETRONIO, C., BELLUCCI, L., DI STEFANO, G. *Axis eurygonos* from Pirro Nord (Apricena, Southern Italy). *Palaeontographica*, 2013, nr. 298, pp. 169-181. ISSN 0375-0442.

326. PETRONIO, C., KRAKHMALNAYA, T., BELLUCCI, L., DI STEFANO, G. Remarks on some Eurasian pliocervines: Characteristics, evolution, and relationships with the tribe Cervini. *Geobios*, 2007, nr. 40, pp. 113-130. ISSN 0251-1223.

327. PETRONIO, C., SARDELLA, R. Biochronology of the Pleistocene mammal fauna from Ponte Galeria (Rome) and remarks on the Middle Galerian faunas. *Rivista Italiana di Paleontologia e Stratigrafia*, 1999, nr. 105(1), pp. 155-164. ISSN 0035-6883.

328. PEVZNER, MA., VANGENGEIM, EA., VISLOBOKOVA, IA. Ruscinian of the territory of the former Soviet Union. *Newsletters on Stratigraphy*, 1996, nr. 33(2), pp. 77-97. ISSN 0078-0421.

329. PFEIFFER, T. *Dama* (*Pseudodama*) *reichenaui* (Kahlke, 1996) (Artiodactyla: Cervidae, Cervini) aus den Mosbach-Sanden (Wiesbaden-Biebrich). *Mainzer Naturwissenschaftliches Archiv*, 1997, nr. 35, pp. 31-59. ISSN 0174-6626.

330. PFEIFFER, T. Die fossilen Damhirsche von Neumark Nord (Sachsen-Anhalt) – *D. dama geiselana* n. ssp. *Eiszeitalter und Gegenwart*, 1998, nr. 48, pp. 72-86. ISSN 0424-7116.

331. PFEIFFER, T. Die Stellung von *Dama* (Cervidae, Mammalia) im System plesiometacarpaler Hirsche des Pleistozäns - Phylogenetische Rekonstruktion - Metrische Analyse. *Courier Forschungsinstitut Senckenberg*, 1999, nr. 211, pp. 1–218. ISSN 0341-4116.

332. PFEIFFER, T. The first complete skeleton of *Megaloceros verticornis* (Dawkins, 1868) Cervidae, Mammalia, from Bilshausen (Lower Saxony, Germany): description and phylogenetic implications. *Mitteilungen des Museums für Naturkunde in Berlin, Geowissenschaftliche Reihe*, 2002, nr. 5, pp. 289-308. ISSN 1435-1935.

333. PFEIFFER, T. The position of *Dama* (Cervidae, Mammalia) in the system of fossil and living deer from Europe–phylogenetical analysis based on the postcranial skeleton. *Quaternaire*, 2005, Hors-série 2, pp.39-57. ISSN 1965-0795.

334. PFEIFFER-DEML, T. Deer from the Pliocene site of Bad Deutsch-Altenburg 26 (Lower Austria, Leithagebirge): Conclusions based on skeletal morphology. *Annalen des Naturhistorischen Museums in Wien. Serie A*, 2016, nr. 118, pp. 133-173. ISSN 0255-0105.

335. PIDOPLITSCHKO, IG. A new form of *Muntiacus* from Pliocene deposits of Southern Ukraine. *Reports of the Academy of Sciences of USSR*, 1951, nr. 31(4), pp. 677-679 (in Russian).

336. PIDOPLITSCHKO, IG., FLEROV, KK. The new form of deer from Pliocene of Southern Ukraine. *Reports of the Academy of Sciences of USSR*, 1952, nr. 84(6), pp. 1239-1242 (in Russian).

337. PITRA, C., FICKEL, J., MEIJAARD, E., GROVES, PC. Evolution and phylogeny of old world deer. *Molecular Phylogenetics and Evolution*, 2004, nr. 33, pp. 880-895. ISSN 1055-7903.

338. POCOCK, RI. December. On Antler-Growth in the Cerviæ, with special reference to *Elaplurus* and *Odocoileus* (*Dorcelaphus*). *Proceedings of the Zoological Society of London*, 1912, nr. 82(4), pp. 773-783.

339. POCOCK, RI. The larger deer of British India. *The Journal of the Bombay Natural History Society*, 1942, nr. 43(3), pp. 298-317.

340. POCOCK, RI. The larger deer of British India, Part II. *The Journal of the Bombay Natural History Society*, 1943a, nr. 43(4), pp. 553-572.

341. POCOCK, RI. The larger deer of British India, Part III. *The Journal of the Bombay Natural History Society*, 1943b, nr. 44(1), pp. 27-37.

342. POCOCK, RI. The larger deer of British India, Part IV. *The Journal of the Bombay Natural History Society*, 1943c, nr. 44(1), pp. 169-178.

343. POHLIG, H. Die Cerviden des thüringischen Diluvial-Travertines mit Beiträgen über andere diluviale und über recente Hirschformen. *Palaeontographica*, 1892, nr. 39, pp. 215-263.

344. POHLIG, H. Über zwei neue altplistocäne Formen von *Cervus*. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 1909, nr. 61, pp. 250-253.

345. POHLIG, H. Über *Cervus loczyi* Pohlig n. sp. In: KADIC, O., ed. Die fossile Säugetierfauna der Umgebung des Balatonsees. *Paläontologische Abhandlungen. Resultate der wisseschaftl. Erforschung des Balatonsees*, 1911, nr. 1, pp. 7-8.

346. POLZIEHN, RO., STROBECK C. Phylogeny of Wapiti, Red Deer, Sika Deer, and Other North American Cervids as Determined from Mitochondrial DNA. *Molecular Phylogenetics and Evolution*, 1998, nr. 10(2), pp. 249-258.

347. POMEL, M. *Catalogue méthodique et descriptif des vertèbres fossiles découverts dans le bassin hydrographique supérieur de la Loire et surtout dans la vallée de son affluent principal, l'Allier*. Paris: Chez J.-B. Bailliere, 1853. 193 p.

348. PORTIS, A. Elenco delle specie di Cervicorni fossili in Roma e attorno a Roma. *Bollettino della Societa Geologica Italiana*, 1920, nr. 39, pp. 132-139.

349. RADULESCO, C. Artiodactyles du Pliocène et du Pléistocène inférieur de Roumanie. *Quaternaire Hors-série*, 2005, nr. 2, pp. 191-200. ISSN 1771-1150.

350. RADULESCU, C., SAMSON, P. Sur un nouveau cerf megacerin du pleistocene moyen de la depression de Brasov (Roumanie). *Geologica Romana*, 1967, nr. 6, pp. 317-344.

351. RADULESCU, C., SAMSON, P., PETCULESCU, A., STIUCA, E. Pliocene Large Mammals of Romania. *Coloquios de Paleontologia*, 2003, Vol. Ext. nr. 1, pp. 549-558. ISSN 1132-1660.

352. RANDI, E., MUCCI, N., PIERPAOLI, M., DOUZERY, E. New phylogenetic perspectives on the Cervidae (Artiodactyla) are provided by the mitochondrial cytochrome b gene. *Proceedings of the Royal Society of London, series B*, 1998, nr. 265, pp. 793-801. ISSN 0080-4649.

353. RANKAMA, T., UKKONEN, P. On the early history of the wild reindeer (*Rangifer tarandus* L.) in Finland. *Boreas*, 2001, nr. 30, pp. 131–147. ISSN 0300-9483.

354. RAVEN, Th. *Megaceros euryceros latifrons* subsp. nov., Beiträge zur Kenntnis der Riesenhirschrassen. *Archief Zeeuwsch Genootschap der Wetenschappen*, 1935, nr. 1935, pp. 179-206.

355. RAY, J. *Synopsis Methodica Animalium Quadrupedum et Serpentini Generis*. London: Impensis S. Smith and B. Walford, 1693. 336 p.

356. RAZOUMOWSKY, G. Sur une tete et des cornes fossiles d'Irlande. *Histoire et Memoires de la Societe des Siences physiques de Lausanne*, 1786, nr. 2, pp. 27-28.

357. REYNOLDS, SH. The Giant Deer. A Monograph of the British Pleistocene Mammalia, Vol. III. Part III. *Monographs of the Palaeontographical Society*, 1929, nr. 81(371), pp. 1-62.

358. RIVALS, F., SOLOUNIAS, N. Differences in Tooth Microwear of Populations of Caribou (*Rangifer tarandus*, Ruminantia, Mammalia) and Implications to Ecology, Migration, Glaciations and Dental Evolution. *Journal of Mammalian Evolution*, 2007, nr. 14, pp. 182-192. ISSN 1064-7554.

359. ROBERT F. Sur les Ossements fossiles des environs de Cussac, commune de Polignac (Haute-Loire). *Annales de la Société d'agriculture, sciences, arts et commerce du Puy*, 1830, nr. 2, pp. 68-88.

360. RØED, KH. Refugial origin and postglacial colonization of Holarctic reindeer and caribou. *Rangifer*, 2005, nr. 25(1), pp. 19-30. ISSN 0333-256X.

361. ROOK, L., MARTINEZ-NAVARRO, B. Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International*, 2010, nr. 219, pp. 134-144. ISSN 1040-6182.

362. RÖSSNER, GE. Odontologische und schädelanatomische Untersuchungen an *Procervulus* (Cervidae, Mammalia). *Münchner geowissenschaftliche Abhandlungen*, 1995, nr. 29, pp. 1-127. ISSN 0177-0950.

363. RUIZ-BUSTOS, A., FERNÁNDEZ, J., MORALES, J., RODRÍGUEZ-FERNÁNDEZ, J., VERA, JA. Bioestratigrafia de los materiales Plio-Cuaternarios del borde norte de la Depresion de Granada. *Estudios geológicos*, 1990, nr. 46(3-4), 277-290. ISSN 0367-0449.

364. RUNDEL, PW., ARROYO, MT., COWLING, RM., KEELEY, JE., LAMONT, BB., VARGAS, P. Mediterranean biomes: evolution of their vegetation, floras, and

climate. *Annual Review of Ecology, Evolution, and Systematics*, 2016, nr. 47, pp. 383-407. ISSN: 1545-2069.

365. RÜTIMEYER, L. *Die Fauna der Pfahlbauten der Schweiz*. Basel: Basel Schweighauser, 1861, 248 p.

366. RÜTIMEYER, L. *Beiträge zu einer natürlichen Geschichte der Hirsche,* Vol. 7. Zürich: Zürcher und Furrer, 1881. 122 p.

367. RUTTEN, LMR. *Die diluvialen säugetiere der Niederlande*. PhD dissertation, University of Utrecht, 1909. 116 p.

368. SABLIN, MV., KUZMINA, I. Late Pleistocene reindeer (*Rangifer tarandus*) from Upper Don Area. *Proceedings of the Zoological Institute*, 1992, nr. 246, pp. 72-80 (in Russian). ISSN 0206-0477.

369. SABOL, M. New findings of Late Pliocene vertebrates from Hajnácka I site (southern Slovakia). *Coloquios de Paleontología*, 2003, Vol. Ext. nr. 1, pp. 595-602. ISSN 1132-1660.

370. SAMEJIMA, Y., MATSUOKA, H.,. A new viewpoint on antlers reveals the evolutionary history of deer (Cervidae, Mammalia). *Scientific reports*, 2020, nr. 10(1), p.8910. ISSN: 2045-2322.

371. SAMSON P., RADULESCO C., KISGYORGY Z. Nouvelles données sur la faune de mammifères du Villafranchien inférieur de Capeni-Vighis (dépression de Braşov, Roumanie). *Eiszeitalter und Gegenwart*, 1970, nr. 22, pp. 64-88.

372. SANZ, M., DAURA, J., BRUGAL, JP. First occurrence of the extinct deer *Haploidoceros* in the Iberian Peninsula in the Upper Pleistocene of the Cova del Rinoceront (Castelldefels, Barcelona). *CR Palevol*, 2014, nr. 13, pp. 27-40. ISSN 16310683, 1777571X.

373. SAVI, F., SISMONDA, A. Sez. Geol. Min. Paleont. *Atti Terza Riunione Sci. Ital. Firenze*, 1841, pp. 107-193.

374. SCHAUB, S. Die kleine hirschart aus dem oberpliocaen von seneze (Haute-Loire). *Eclogae Geologica Helvetiae*, 1941, nr. 34(2), pp. 264-271.

375. SCHILLING, AM., RÖSSNER, G. New skull material of Pleistocene dwarf deer from Crete (Greece). *CR Palevol*, 2021, nr. 20(9), pp. 141-164. ISSN 16310683, 1777571X.

376. SCHLOSSER, M. Die fossilen Säugethiere Chinas, nebst einer Odontographie der recenten Antilopen. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften*, 1903, nr. 22(1), pp. 3-221.

377. SCHLOSSER, M. Tertiary vertebrates from Mongolia. *Palaeontologia Sinica - Series C*, 1924, nr. 1(1), pp. 1-119.

378. SCHMIDT-KITTLER, N., 1989. A Biochronologic Subdivison of the European Paleogene Based on Mammals. In: Lindsay EH., Fahlbusch V., Mein P., eds. *European Neogene Mammal Chronology. NATO ASI Series – Series A: Life Sciences*, 1989, nr. 180, pp. 47-50. ISBN 978-1-4899-2515-2.

379. SCHREUDER, A. The Tegelen fauna, with a description of new remains of its rare components (*Leptobos*, *Archidiskodon meridionalis*, *Macaca*, *Sus strozzii*). Archives *Néerlandaises de Zoologie*, 1946, nr. 7(1), pp. 153-204.

380. SCOTT, KM. Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the Americal Museum of Natural History*, 1985, nr. 179, pp. 197-288. ISSN 0003-0090.

381. SERRES, DE M. Note sur les animaux des terrains tertiaires marins supérieurs découverts dans le sol immergé des environs de Montpellier. *Annales des sciences naturelles, seconde serie*, 1838, nr. 9, pp. 280-292.

382. SEVERTZOFF, NA. Altitudinal and latitudinal distribution of Turkestan animals. *Proceedings of the Imperial Society of Naturalists, Anthropologists, and Ethnographists*, 1873, nr. 8(2), pp. 1-157 (in Russian).

383. SEVERTZOFF, NA. The Mammals of Turkestan. *The Annals and Magazine of Natural History, including Zoology, Botany, and Geology*, 1876, nr. 18 (4), pp. 377-388.

384. SIGOGNEAU, D. Edude d'un cervidé pléistocène de Corse. *Annales de paléontologie*, 1960, nr. 46, pp. 49-77.

385. SIMIONESCU, I. Vertebrate pliocene de la Malusteni (Covurlui). *Academia Romana, publicatiunile fondului Vasile Adamachi*, 1930, nr. 9 (49), pp. 83-151.

386. SIMIONESCU, I., DOBRESCU, E. Mamiferele Pliocene dela Cimișlia (Basarabia). V. Rumegătoarele. *Academia Română, Publicațiunile Fondului Vasile Adamachi*, 1941, nr. 9(54), pp. 1-36.

387. SIMONELLI, V. Mammiferi quaternari dell'Isola di Candia. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna, Classe di Scienze Fisiche*, 1907, nr. 6(4), pp. 455-471.

388. SIMPSON, GG. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 1945, nr. 85, pp. 1-350.

389. SCHARFF, RF., SEYMOUR, HJ., NEWTON, ET. The Exploration of Castlepook Cave, County Cork, Being the Third Report from the Committee Appointed to Explore

Irish Caves. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, 1917, nr. 34, pp. 33-72.

390. SCHMIDT-KITTLER, N. A biochronologic subdivision of the European Paleogene based on mammals – report on results of the Paleogene Symposium held in Mainz in February 1987. In: LINDSAY, EH., FAHLBUSCH, V., MEIN, P., eds. *European Neogene Mammal Chronology. NATO ASI Series – Series A: Life Sciences*, 1989, nr. 180, pp. 47-50. ISBN 978-1-4899-2513-8.

391. SCHROEBER J. Ch. D. von. *Der Säugetiere in Abbildungen nach der Natur*. 1836, Abteilung 5, Erlangen, pp. i-vi, 939-1839

392. SOBOLEV, A. Posttertiäre Säugethiere. 1. Hufthiere. A. Elenthiere. *Beschreibung der sammlungen des museums in Krasnojarsk. Palaontologischer teil*, 1914, nr. 1, pp. 1-17 (in Russian with German summary).

393. SOERGEL, W. *Cervus megaceros mosbachensis* n. sp. und die Stammesgeschichte der Riesenhirsche. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 1927, nr. 39(4), pp. 365-407.

394. SOKOLOV, II. *Hoofed animals (Perissodactyla and Artiodactyla). Fauna of the USSR. Mammalia 1 (3)*. Moscow: Academy of Sciences of USSR, 1959. 640 p. (in Russian).

395. SOLOUNIAS, N., MOELLEKEN, SM. Dietary adaptation of some extinct ruminants determined by premaxillary shape. *Journal of Mammalogy*, 1993, nr. 74(4), pp.1059-1971. ISSN 00222372.

396. SOMMER, RS., ZACHOS, FE., STREET, M., JÖRIS, O., SKOG, A., BENECKE, N.. Late Quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe. *Quaternary Science Reviews*, 2008, nr. 27(7-8), pp. 714-733. ISSN 0277-3791.

397. SONDAAR, PY. Insularity and its effect on mammal evolution. In: Hecht, MK., Goody, PC., Hecht, BM., *Major patterns in vertebrate evolution*. Boston, MA: Springer US, 1977. pp. 671-707. ISBN: 978-1-4684-8853-1

398. SUTULA, VA. Adaptation significance of proportions of the ungulates. *Transactions of the Zoological Institute*, 1990, nr. 215, pp. 137-151 (in Russian). ISSN 03735893.

399. SPAAN, A. A revision of the deer from Tegelen (Province of Limburg, The Netherlands). *Scripta Geologica*, 1992, nr. 98, pp. 1-42. ISSN 0375-7587.

400. SPASSOV, N. Brief review of the Pliocene ungulate fauna of Bulgaria. *Quaternaire, Hors-série*, 2005, nr. 2, pp. 201-212. ISSN 1771-1150.

401. STANKOVIC, A., DOAN, K., MACKIEWICZ, P., RIDUSH, B., BACA, M., GROMADKA, R., SOCHA, P., WEGLENSKI, P., NADACHOWSKI, A., STEFANIAK, K. First ancient DNA sequences of the Late Pleistocene red deer (*Cervus elaphus*) from the Crimea, Ukraine. *Quaternary International*, 2011, nr. 245(2), pp. 262-267. ISSN 1040-6182.

402. STEENSMA, KJ. *Plio-IPleistozane Großsäugetiere (Mammalia) aus dem Becken von Kastoria I Grevena, südlich von Neapolis - NW Griechenland*. Inaugural-Dissertation, Technische Universität Clausthal-Zellerfeld, 1988. 315 p.

403. STEFANIAK, K. Late Pliocene cervids from Węże 2 in southern Poland. *Acta Palaeontologica Polonica*, 1995, nr. 40(3), pp. 327-340. ISSN 0567-7920.

404. STEFANIAK, K. *Jelenie (Cervidae, Mammalia) z dolnego i oerodkowego plejstocenu Polski*. PhD thesis. Archiwum Uniwersytetu Wroclawskiego, 2001. 123 p.

405. STEFANIAK, K. Early and Middle Pleistocene elk (Alcinae Jerdon, 1874, Cervidae, Mammalia) from Poland. *Acta zoologica cracoviensia*, 2007, nr. 50A(1-2), pp. 73-92. ISSN 2300-0163.

406. STEFANIAK, K. 2015. *Neogene and Quaternary Cervidae from Poland*. Krakow: Institute of Systematics and Evolution of Animals Polish Academy of Sciences, 204 p. ISBN 9788361358640.

407. STEHLIN, HG. Les sables de Rosières, près Saint-Florent (Cher). II. Paléontologie. *Bulletin de la Société Géologique de France. 4e serie*, 1912, nr. 12, pp. 198-212.

408. STEININGER, FF., BERNOR, RL., FAHLBUSCH, V. European Neogene marine/continental chronologic correlations. In: LINDSAY, EH., FAHLBUSCH, V., MEIN, P., eds. *European Neogene Mammal Chronology. NATO ASI Series – Series A: Life Sciences*, 1989, nr. 180, pp. 15-46. ISBN 978-1-4899-2515-2.

409. SYMEONIDIS, NK. Ein Vollständiges Geweih von *Pliocervus pentelici* (Gaudry) aus Pikermi (Griechenland). *Annales Géologiques des Pays Helléniques*, 1974, nr. 23, pp. 308-316.

410. TEILHARD DE CHARDIN, P., PEI, WC. The fossil mammals from locality 13 of Choukoutien. *Palaeontologia Sinica. New Series C*, 1941, nr. 11, pp. 1-119.

411. TEILHARD DE CHARDIN, P., PIVETEAU, J. Les mamiferes fossiles de Nihovan (Chine). *Annales de Paleontologie*, 1930, nr. 19, pp. 5-132.

412. TEILHARD DE CHARDIN, P., TRASSAERT, M. The Pliocene Camelidae, Giraffidae and Cervidae of south eastern Shansi. *Palaeontologia Sinica, C,* 1937, nr. 1 (new series), nr. 102 (whole series), pp. 1-68.

413. THOMAS, H. La faune quaternaire d'Algerie. *Archeologia*, 1979, nr. 134, pp. 61-71. ISSN 0570-6270.

414. THOMAS, JM. *Eostyloceros pierensis* nov. sp., nouveau cervuline du Pontien europeen. *Comptes Rendus Sommaires des Seances de la Societe Geologique de France*, 1951, nr. 6, pp. 255-257.

415. TITOV, VV., SHVYREVA, AK. Deer of the Genus *Megaloceros* (Mammalia, Cervidae) from the Lower Pleistocene of Ciscaucasia. *Paleontological Journal*, 2016, nr. 2016(1), pp. 82-90. ISSN 0031-0301.

416. TORCAPEL, A. Le plateau des Coirons (Ardèche) et ses alluvions sous-basaltiques. *Bulletin de la Société Géologique de France*, 1882, nr. 10(3), pp. 406-420.

417. TROUESSART, EL. *Catalogus mammalium tam viventium quam fossilium.* Vol. 1. Berolini, R. Friedländer & sohn: 1899. 664 p.

418. VALLI, A. Dispersion of the genus *Procapreolus* and the relationships between *Procapreolus cusanus* and the roe deer (*Capreolus*). *Quaternary International*, 2010, nr. 212, pp. 80-85. ISSN 1040-6182.

419. VALLI, A., GUERIN, C. Le gisement pleéistocène supérieur de la grotte de Jaurens à Nespouls, Corrèze, France: les cervidae (Mammalia, Artiodactyla). *Cahiers scientifiques, Muséum de Lyon*, 2000, nr. 1, pp. 41-81. ISSN 2823-2437.

420. VALLI, A., PALOMBO, MR. Le régime alimentaire du Cervidae (Mammalia) *Eucladoceros ctenoides* (Nesti, 1841) reconstitué par la morphologie du crâne et par l'usure dentaire. *Eclogae Geologicae Helvetiae*, 2005, nr. 98 (1), pp. 133-143. ISSN 0012-9402.

421. VAN DER GEER, AAE. Island ruminants and parallel evolution of functional structures. *Quaternaire*, 2005, nr. 2, pp.231-240. ISSN 1965-0795.

422. VAN DER GEER, AAE. Uniformity in variety: Antler morphology and evolution in a predator-free environment. *Palaeontologia Electronica*, 2018, nr. 21.1.9A, pp. 1-31. https://doi.org/10.26879/834palaeo-electronica.org/content/2018/2159-uniformity-in-variety. ISSN 1094-8074.

423. VAN DER MADE, J. Ungulates from gran Dolina (Atapuerca, Burgos, Spain). *Quaternaire*, 1998, nr. 9 (4), pp. 267-281. ISSN 1965-0795.

424. VAN DER MADE, J. Artiodactyla del yasimento mesopleistoceno de Galeria (Sierra de Atapuerca). *Arqueologia en Castilla y Leon, Memorias*, 1999, nr. 7, pp. 143-167.

425. VAN DER MADE, J. *Megaloceros giganteus* from the Middle Pleistocene of Neumark-Nord. In: JUSTUS, A., FIEDLER, L., BURDUKIEWICZ, JM., HEINRICH, WD., BRÜHL, E., eds. *Erkenntnisjäger: Kultur und Umwelt des frühen Menschen. Festschrift für Dietrich Mania, Veröffentlichungen des Landesamtes für Archäologie Sachsen-Anhalt – Landesmuseum für Vorgeschichte*, 2003, nr. 57 (II), pp. 373-378. ISBN 3-910010-69-5.

426. VAN DER MADE, J. The evolution and biogeography of the Pleistocene giant deer *Megaloceros giganteus* (Cervidae, Mammalia). *Courrier Forsch.-Institut Senckenberg*, 2006, nr. 256, pp. 117-129. ISSN 0341-4116.

427. VAN DER MADE, J. The latest Early Pleistocene giant deer *Megaloceros novocarthaginiensis* n. sp. and the fallow deer "*Dama* cf. *vallonnetensis*" from Cueva Victoria (Murcia, Spain). *Mastia: Revista del Museo Arqueológico Municipal de Cartagena*, 2014, nr. 11, pp. 269-323. ISSN 1579-3303.

428. VAN DER MADE, J. The dwarfed “giant deer” *Megaloceros matritensis* n. sp. from the Middle Pleistocene of Madrid – a descendant of *M. savini* and contemporary to *M. giganteus*. *Quaternary International*, 2019, nr. 520, pp. 110-139. ISSN 1040-6182.

429. VAN DER MADE, J., PALOMBO, MR. *Megaloceros sardus* n. sp., a large deer from the Pleistocene of Sardinia. *Hellenic Journal of Geosciences*, 2005, nr. 41 (1), pp. 163-176. ISSN 1105-0004.

430. VAN DER MADE, J., TONG, HW. Phylogeny of the giant deer with palmate brow tines *Megaloceros* from west and *Sinomegaceros* from east Eurasia. *Quaternary International*, 2008, nr. 179, pp. 135-162. ISSN 1040-6182.

431. VANGENGEIM, EA., PEVZNER, MA., TESAKOV, AS. Ruscinian and Lower Villafranchian: Age of Boundaries and Position in Magnetochronological Scale. *Stratigraphy and Geological Correlation*, 2005, nr.13 (5), pp. 530-546. ISSN 0869-5938.

432. VANGENGEIM, EA., VISLOBOKOVA, IA., SOTNIKOVA, MV. Large Ruscinian mammals on the territory of former USSR. *Stratigraphy and Geological Correlation*, 1998, nr. 6 (4), pp. 52-66 (in Russian). ISSN 0869-5938.

433. VAN KOLFSCHOTEN, T., VAN DER JAGT, I., BEEREN, Z., ARGIT,I V., VAN DER LEIJE, J., VAN ESSEN, H., BUSSCHERS, FS., STOEL P., VAN DER PLICHT, H.. A remarkable collection of Late Pleistocene reindeer (*Rangifer tarandus*) remains from

Woerden (The Netherlands). *Quaternary International*, 2011, nr. 238, pp. 4-11. ISSN 1040-6182.

434. VEKUA, A., BENDUKIDZE, O., KILADZE, S. Gigantic deer in Plio-Pleistocene. *Proceedings of Georgian National Museum, natural and prehistoric section*, 2010, nr. 2, pp. 38-53 (in Georgian). ISSN 1987-7412.

435. VERESCHAGIN, NK. Remains of mammals from the lower Quaternary deposits of the Tamanian peninsula. *Transactions of the Zoological Institute*, 1957, nr. 22, pp. 9-74 (in Russian).

436. VERESCHAGIN, NK. *Mammals of Caucasus (history of faunal development)*. Moscow-Leningrad: Academy of Sciences of USSR, 1959. 704 p. (in Russian).

437. VERESTCHAGIN, NK. The Caucasian elk (*Alces alces caucasicus* N. Ver. subsp. nova) and contributions to the natural history of elks on Caucasus. *Zoological Journal*, 1955, nr. 34 (2), pp. 460-463 (in Russian).

438. VIRET, J. Artiodactyla. *Traite de Paleontologie*, t. 6, v. 1. Paris: Masson et Cie, 1961, pp. 887-1084.

439. VISLOBOKOVA, IA. On systematical position of the deer from Pavlodar and the origin of neocervines. *Paleontological journal*, 1980, nr. 3, pp. 91-106 (in Russian). ISSN 0031-0301.

440. VISLOBOKOVA, IA. The Fossil deer of Mongolia. *Transactions of the Joint Soviet-Mongolian paleontological expedition,* 1983, nr. 23, pp. 5-78 (in Russian). ISBN 978-5-907036-09-3.

441. VISLOBOKOVA, IA. Elks in the Pliocene of the USSR. *Quartärpaläontologie*, 1986, nr. 6, pp. 239-242. ISSN 0138-3116.

442. VISLOBOKOVA, IA. The fossil deer of Eurasia. *Transactions of Paleontological Institute*, 1990, nr. 240, pp. 1-208 (in Russian). ISBN 5-02-004695-7.

443. VISLOBOKOVA, I. On Pliocene faunas with Proboscideans in the territory of the former Soviet Union. *Quaternary International*, 2005, nr. 126, pp. 93-105. ISSN: 1040-6182.

444. VISLOBOKOVA, IA. A new species of Megacerini (Cervidae, Artiodactyla) from the late Miocene Taralyk-Cher, Tuva (Russia), and remarks on the relationships of the group. *Geobios*, 2009, nr. 42, pp. 397-410. ISSN 0016-6995.

445. VISLOBOKOVA, IA. 2012. Giant Deer: Origin, Evolution, Role in the Biosphere. *Paleontological Journal*, 46 (7): 643-775. ISSN 0031-0301.

446. VISLOBOKOVA, IA. Morphology, Taxonomy, and Phylogeny of Megacerines (Megacerini, Cervidae, Artiodactyla). *Paleontological Journal*, 2013, nr. 47 (8), pp. 833-950. ISSN 0031-0301.

447. VISLOBOKOVA, I., DMITRIEVA, E., KALMYKOV, N. 1995. Artiodactyls from the Late Pliocene of Udunga, Western Trans-Baikal, Russia. *Journal of Vertebrate Paleontology*, 15 (1): 146-159. ISSN 0272-4634.

448. VISLOBOKOVA, IA., KALMYKOV, NP. On history of roe deer. In: *Paleoteriologia.* Moscow: Nauka, 1994, pp. 214-235 (in Russian).

449. VISLOBOKOVA, IA., TITOV, VV., LAVROV, AV., STARTSEV, DB., TARASENKO, KK., LOPATIN, AV. On the occurrence of giant deer of the genus *Arvernoceros* at Taurida Cave in Crimea. *Doklady Akademii Nauk*, 2019, nr. 487 (5), pp. 596-599. ISSN 0869-5652.

450. VÖRÖS, I. *Alces brevirostris* Kretzoi from the Ördöglyuk Cave at Solymar (Hungary). *Fragmenta mineralogical et palaeontologica*, 1985, nr. 12, pp. 59-66. ISSN 0367-2697.

451. DE VOS, J. The endemic Pleistocene deer of Crete. *Verhandelingen der Koninklijke Akademie van Wetenschappen afd. Natuurkunde. Eerste Reeks*, 1984, nr. 31, pp. 1-100. ISSN 0373-4668.

452. VOS, J. DE, MOL, D., REUMER, JWF. Early pleistocene Cervidae (Mammalia, Artyodactyla) from the Oosterschelde (the Netherlands), with a revision of the cervid genus *Eucladoceros* Falconer, 1868. *Deinsea*, 1995, nr. 2: 95-121. ISSN 2468-8983.

453. WANG, L.-H., ZHANG, Z.-Q. Late Miocene *Cervavitus novorossiae* (Cervidae, Artiodactyla) from Lantian, Shaanxi Province. *Vertebrata PalAsiatica*, 2014, nr. 52(3), pp. 303-315. ISSN 2096-9899.

454. WEBB, DS. Evolutionary History of New World Cervidae. In: VRBA, ES., SCHALLER, GB., eds. *Antelopes, Deer, and Relatives*. New York: Wildlife Conservation Societyn, 2000, pp. 38-64. ISBN 0300081421

455. WILLEMSEN, G. De evolutie van het rendier. *Cranium,* 1984, nr. 1 (2), pp.55-62.

456. WRIGHT, T. *Louthiana: or, an introduction to the antiquities of Ireland*. London: W. Faden, 1748, 20 p.

457. ZDANSKY, O. Fossile Hirsche Chinas. *Palaeontologia Sinica*, Series C, 1925, nr. 2 (3), pp. 1-94.

458. ZITTEL, VON KA. *Palaeozoologie: Vertebrata (Mammalia). 4* (Vol. 1). Munich - Leipzig: Oldenbourg. 1893. 819 p.

APPENDICES

Appendix 1. Tables

Tab. A.1. ***Procapreolus cusanus*** **(Croizet and Jobert, 1828): measurements of the antlered braincase from the collection of MNHN, Paris (the type specimen of** ***Cervus buladensis*****)**

Measurements	**mm**
Frontal breadth	64.0
Breadth behind pedicles	57.6
Maximal breadth of braincase	67.5
Breadth of occiput	72.4
Height of occiput	48.2
Breadth of occipital condyles	39.3
Length of pedicle (sin/dx)	26.0 / 27.2
DAP pedicle (sin/dx)	19.2 / 18.8
DAM pedicle (sin/dx)	20.6 / 20.0
DAP burr (sin/dx)	36.5 / 31.0
DLM burr (sin/dx)	38.4 / 32.9
DAP above burr (sin/dx)	26.2 / 21.2
DLM above burr (sin/dx)	26.0 / 22.3
L orbit – pedicle (sin)	56.2

Tab. A.2. Measurements of antlers and pedicles of ***Damacerus bessarabiae*** **Khomenko, 1913 (the type specimens from Taraclia and the shed antler from Chisla) and** ***Neomegaloceros gracilis*** **from Ananiev (the cast of holotype)**

Measurements	***Damacerus bessarabiae***			***Neomegaloceros gracilis***
	Nr 2384-494, Taraclia	**Nr 2384-579, Taraclia**	**OF 1331, Chisla**	**cast of holotype** (MNHK)
L pedicle	53.0			20.0
DAP pedicle	21.3	21.0		29.7
DLM pedicle	20.5	22.0		31.8
H of ramification	72.0	67.0	135.2	114.0
DAP antler base	21.5	25.0	27.0	33.5
DLM antler base	15.6	16.5	26.0	30.7

Tab. A.3. Cranial measurements of the antlered skull Nr. 43-1612 of *Metadicrocerus variabilis* (Aleksejev, 1913)

Measurements	**left side**	**right side**
L upper cheek teeth P^2-M^3		73.7
L molar series M^1-M^3		41.2
L premolar series P^2-P^4		36.3
D at M^3	82.0	
D at P^2	59.5	
D at orbits	104.0	
D at frontal constriction	106.5	
D of braincase behind pedicles	84.8	
DAP of pedicle	31.2	32.4
DLM of pedicle	32.0	33.1
H of pedicle	23.6	23.6

Tab. A.4. Cranial measurements of *Alces gallicus* and *Alces latifrons*; (r), right; (l), left

Measurements (mm)	*A. gallicus*, holotype (Nr. 96134, PMUL)	*A. gallicus*, East Runton (M6101, NHML)	*A. latifrons*, Mundesley (M6553, NHML)
Frontal breadth		ca. 216.8	ca. 281.4
L P^2-M^3	129.0		
D behind pedicles		111.0	129.5
L bregma – inion		105.8	151.5
H basion – inion	115.2	111.4	144.4
D occipital	168.6	162.7	250.0
D occipital condyles	83.9	85.3	131.1
L P^2 – prosthion	ca. 163.0		
L antler	1160.+ (r)		
D dorsoventral pedicle	62.6 (r)	63.2 (l)	95.5 (l)
DAP pedicle	70.5 (r)	75.1 (l)	113.9 (l)
CFR pedicle	230.0 (r)	230.0 (l)	345.0 (l)
D dorsoventral above burr	65.6 (r)	59.0 (l)	95.3 (l)
DAP above burr	66.4 (r)	67.6 (l)	101.4 (l)
CFR antler base	209.0 (r)	200.0 (l)	320.0 (l)

Tab. A.5. Measurements of the holotype of *Rangifer tarandus tournalii* (De Serres, 1829) from the Tournal (Bize) Cave

Measurements	mm
H of antler ramification above the burr	180
DAP pedicle	51.0
DLM pedicle	43.4
DAP antler base	48.1
DLM antler base	45.2
DAP of antler below ramification	65.0
DLM of antler below ramification	37.0

Tab. A.6. Measurements of cranial fragments of *Rucervus* (*Arvernoceros*) *ardei* Croizet and Jobert, 1828 from Etouaires, France

Measurements	PET1053		PET1052		PET1020	Slobozia Mare
	left	right	left	right	right	
D at frontal constriction	122.0		110.3			
D behind pedicles	99.1					
L bregma – opisthocranion	78.7					
D of occiput	134.6					
H of occiput	81.0					
D of occipital condyles	72.4					
H of pedicle	25.0	24.4	31.5		35.0	
DAP of pedicle	47.7	51.8	42.5		38.3	
DLM of pedicle	50.6	48.7	50.8		40.0	
H first ramification			137.0	134.5	134.0	71.0
DAP of antler above burr	63.1		56.2		48.0	27.3
DLM of antler above burr	54.0		51.0			28.6

Tab. A.7. Measurements of mandibles of large-sized deer (mm)

Species	*Cervus canadensis*	*Praemegaceros solilhacus*	*Praemegaceros pliotarandoides*	*Rucervus gigans*	*Rucervus sp.*	*Eucladoceros dicranios*
Site	Soleilhac	Soleilhac	Apollonia-1	Apollonia-1	Liventsovka	Liventsovka
Collection number	2003-4-420-SOL	2003-4-439-SOL	APL-402 (sin)	APL-384	LIV-836-1810/3	LIV-604-1801/9
L P_2-M_3	151.8	156.3	176.0	188.0	143.8	119.0
L P_2-P_4	57.0	61.3	68.7	73.3	55.0	47.6
L M_1-M_3	94.3	98.8	103.0	116.4	90.0	73.1
L mandible		≈380.0				
L diastema	125.0	105.0		≈ 95.0	102.1	
L P_2 - for. ment.	74.0	48.5	52.0	72.5	55.0	44.0
H diastema	25.3	21.2	22.5	23.8	22.6	16.7
H / P_2	47.7	43.3		37.7	34.6	27.8
H / M_1	48.5	50.6		43.1	41.3	33.3
H / M_2-M_3	51.0	54.0		50.7	45.6	38.2
D / P_2	17.6	17.2		16.5	14.2	12.5
D / M_1	27.3	26.5	19,9	25.4	20.5	17.4
D / M_2-M_3	31.3	29.8	23.4	28.1	23.2	20.6

Appendix 2. Figures.

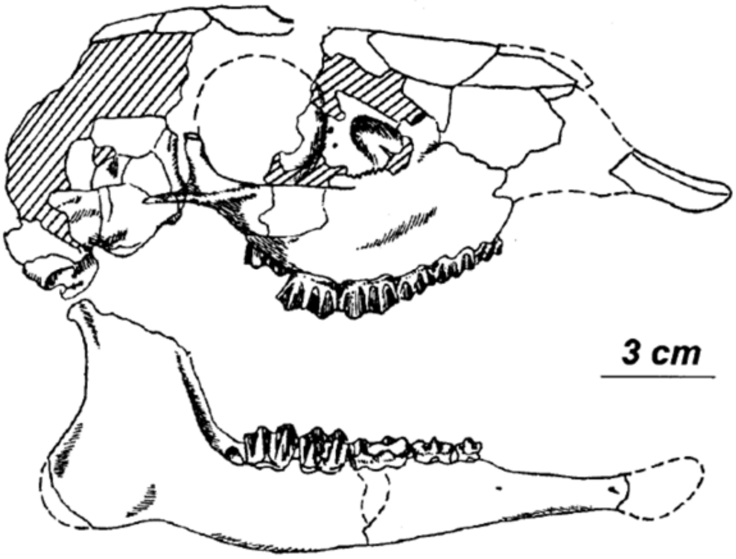

Fig. A.1. The holotype skull of *Procapreolus moldavicus* (Janovskaya, 1957) from Lebedenco (= Fagadil), Cahul district, Moldova

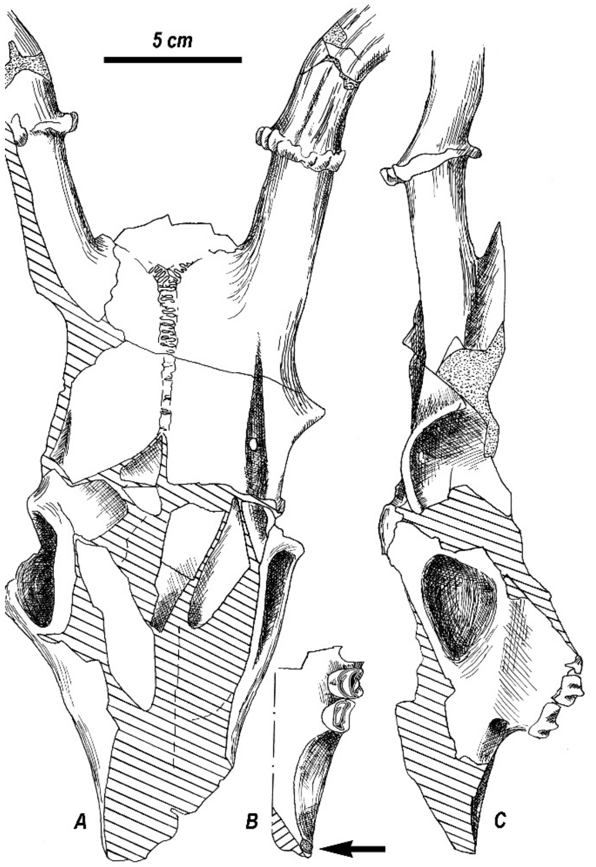

Fig. A.2. *Procapreolus moldavicus* (Janovskaya, 1954): the male skull Nr. 220 (IZW) from Węże-1 (Poland); A, the frontal view; B, the palatal view of rostral part (the alveolus of the upper canine is indicated by the arrow); C, the side view

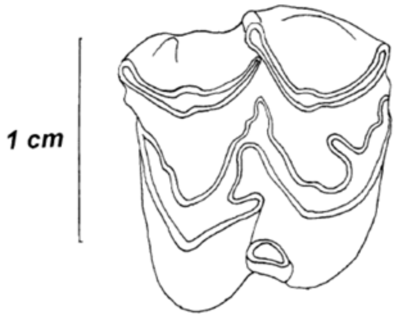

Fig. A.3. The isolated M$^{1-2}$ (Nr. 77, IZC) of *Procapreolus moldavicus* (Janovskaya, 1954) from Tatareşti, Moldova

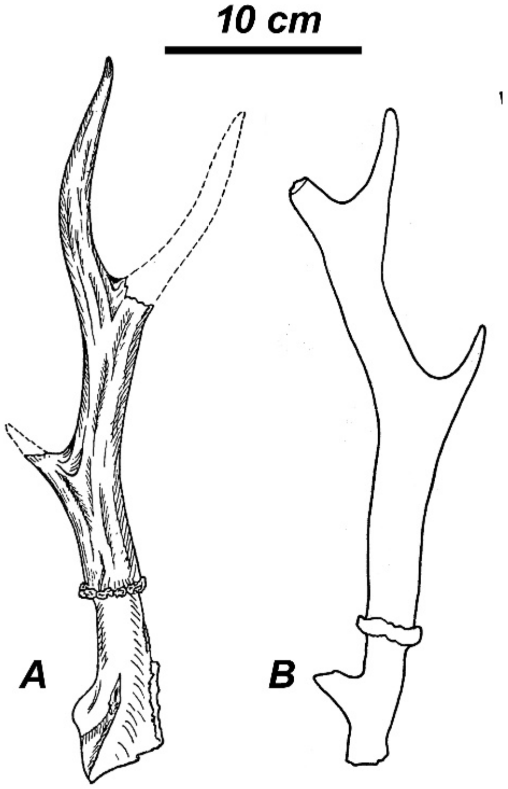

Fig. A.4. A, the holotype of *Procapreolus vesti* Korotkevich, 1970 (adapted from Korotkevich 1970); B, the neotype of *Procapreolus cusanus* (Croizet & Jobert, 1928) (adapted from Heintz 1970)

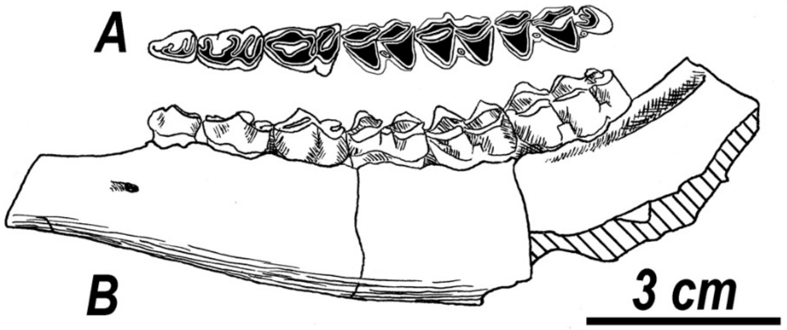

Fig. A.5. ***Procapreolus cusanus*** **(Croizet & Jobert, 1828) from Ravine Les Etouaires (Issoire, France): the left ramus of mandible Nr. 5237, MNHN ("Collection of Croizet"). A, the occlusion view of lower tooth row; B, the lateral view of mandible**

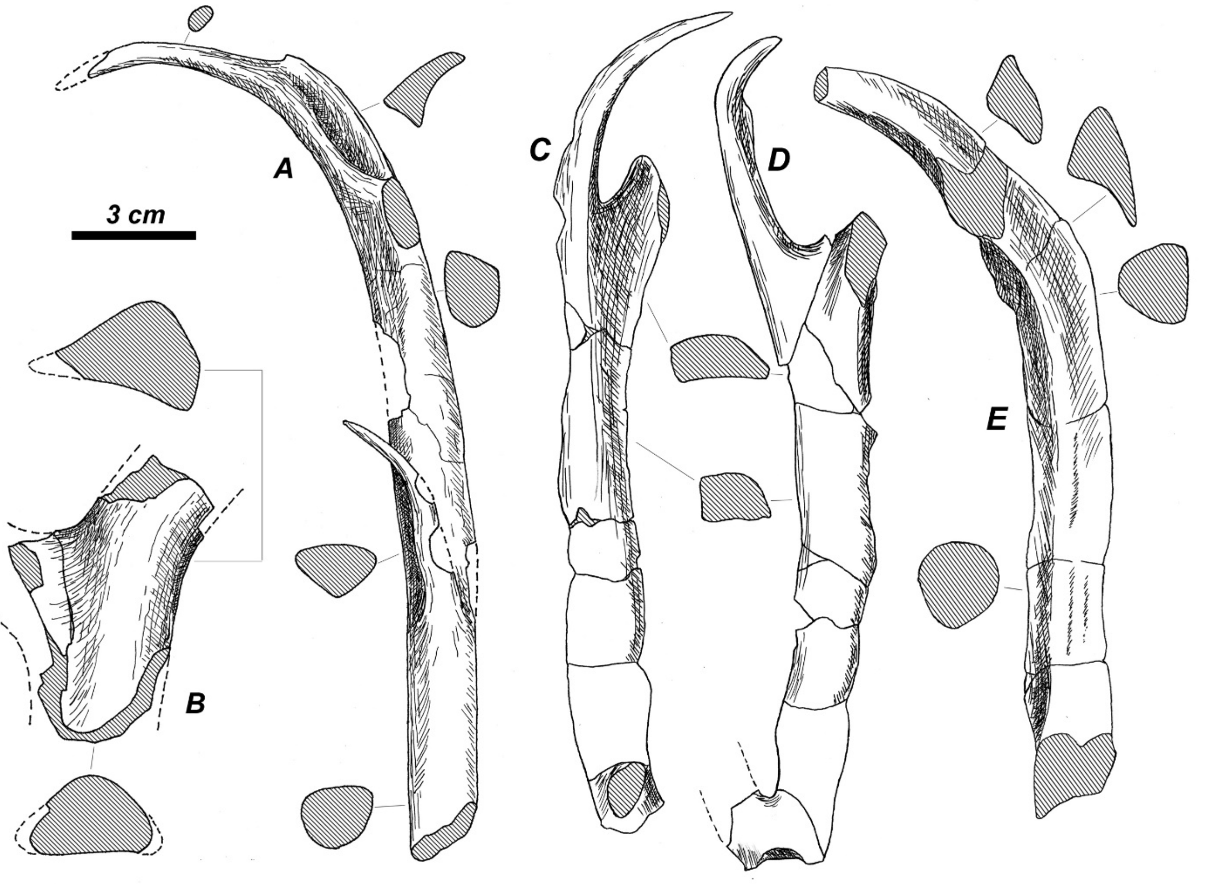

Fig. A.6. Antler fragments of ***Pliocervus matheroni*** **(Gervais, 1852) from Cucuron, France: A, left antler LUB-783 (anterior view) with transversal cross-sections; B, fragment of left ramification with transversal cross-sections; C, LUB-782 (anterior view); D, LUB-782 (medial view); E, LUB-784 (anterior view)**

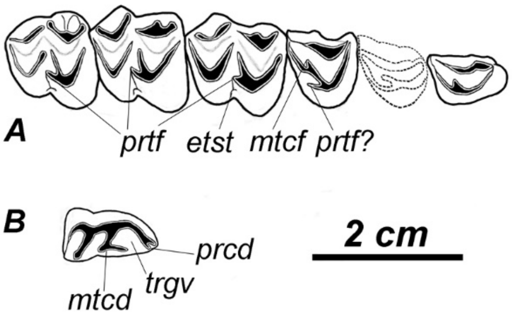

Fig. A.7. Dental morphology of *Pliocervus matheroni* (Gervais, 1852) from Cucuron: A, occlusion view of the upper right incomplete tooth tow (P^2, P^4-M^3) LUB-798; B, occlusion view of lower fourth premolar (P_4) LUB-812; *prtf*, protoconal fold; *etst*, entostyle; *mtcf*, metaconule fold; *mtcd*, metaconid; *trgv*, trigonid valley; *prcd*, paraconid

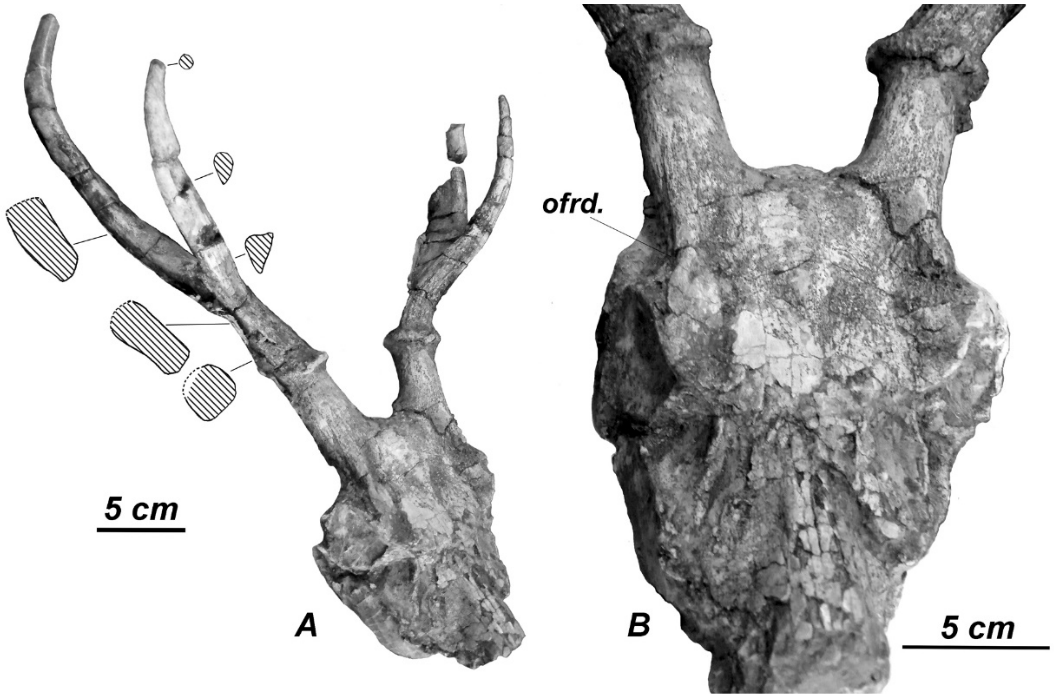

Fig. A.8. The antlered skull of *Damacerus bessarabiae* Khomenko, 1913 from Cimişlia (no number, PMUB): A, Right- side oblique view with transversal antler cross- sections; B, frontal view of skull; *ofrd.*, orbito- frontal ridge

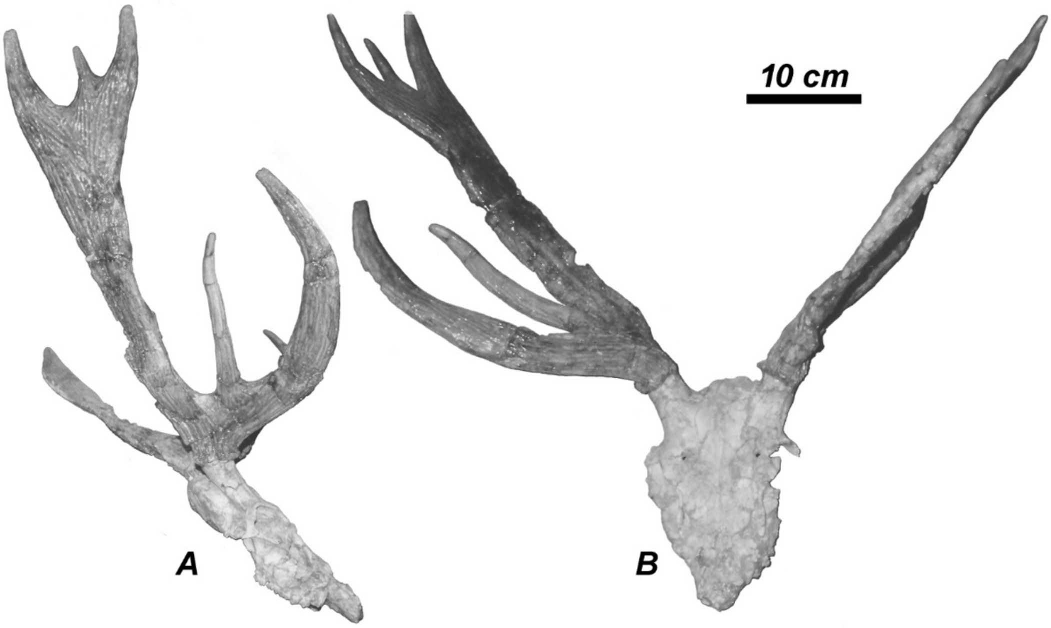

Fig. A.9. Antlered skull Nr. 43-1612 of *Metadicrocerus variabilis* (Aleksejev, 1913) from the Late Miocene of Novoelizavetovka, Ukraine: A, side view; B, frontal view

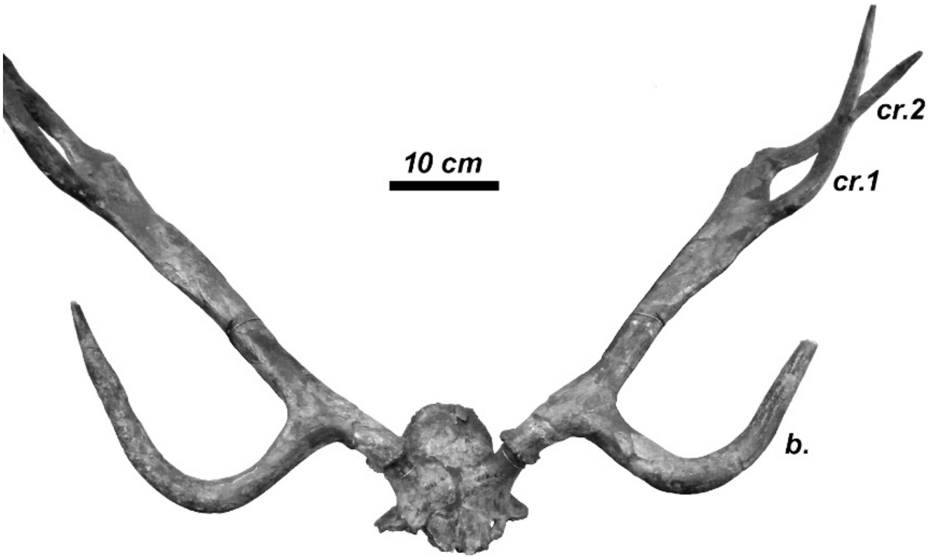

Fig. A.10. The antlered skull Nr. 1923-4 (MNHN) of *Croizetoceros ramosus* (Croizet & Jobert, 1828) from Sénèze

Fig. A.11. The left ramus of the mandible Nr. 3286/5 (SMNH) of *Alces sp.* from Mosbach (Germany). A, the side view of the mandible; B, the occlusion surface of the tooth row. Note the complete fusion of the metaconid and paraconid in P_3.

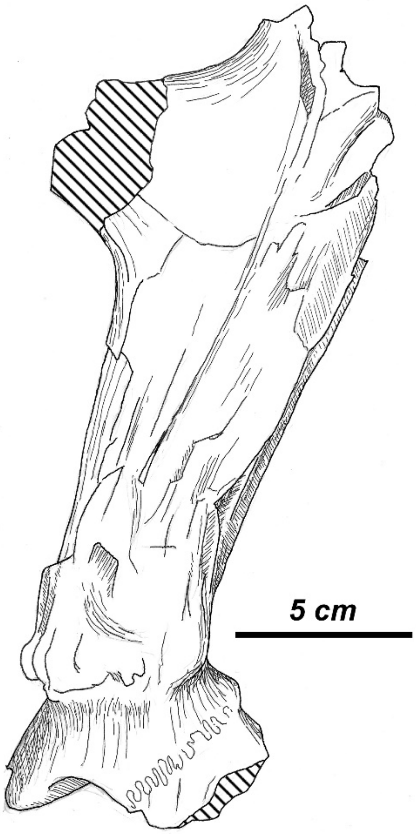

Fig. A.12. The right antler of *Rangifer tarandus tournalii* (De Serres, 1829), holotype

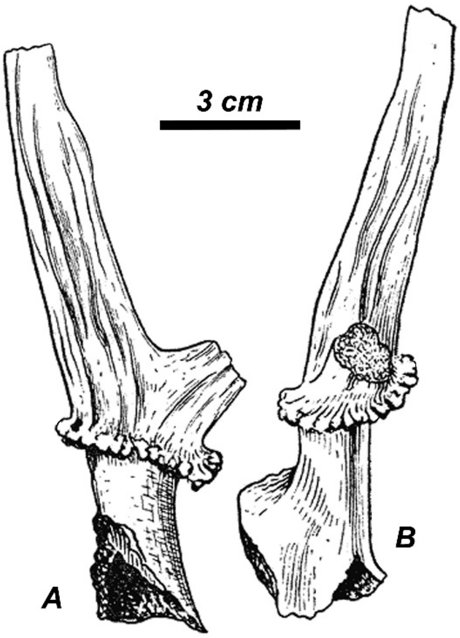

Fig. A.13. ***Praemuntiacus pidoplitschkoi*** **(Korotkevich, 1964): the left antler with pedicle from the Kuchurgan Gravel, Ukraine: A, the median view; B, the anterior view (adapted from Kototkevich, 1965)**

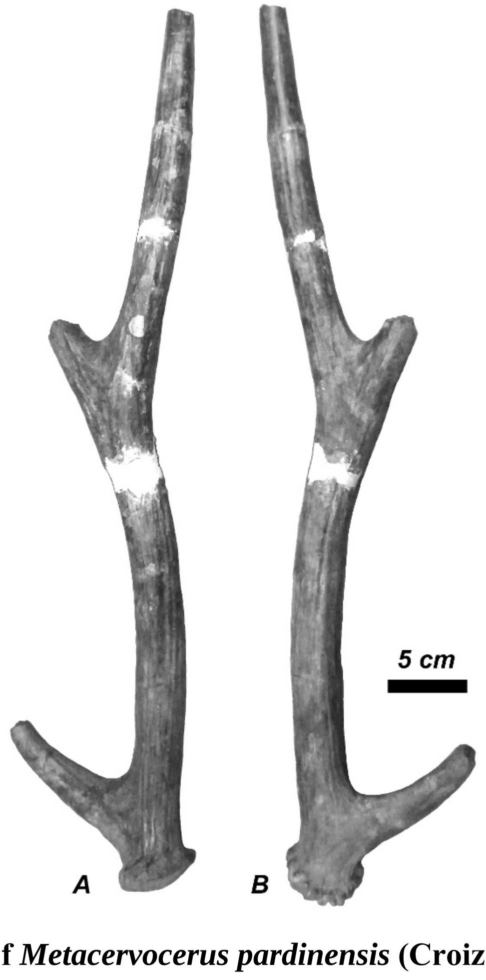

Fig. A.14. The neotype of ***Metacervocerus pardinensis*** **(Croizet & Jobert, 1828) from Perrier-Etouaires, France (MNHN, Paris): A, the lateral view; B, the median view**

Fig. A.15. The antlered male skull CEY-2-2318 (Museum of Prehistory of Les Eyzies-de-Tayac) of *Metacervocerus rhenanus* (Dubois, 1904) from Ceyssaguet, France

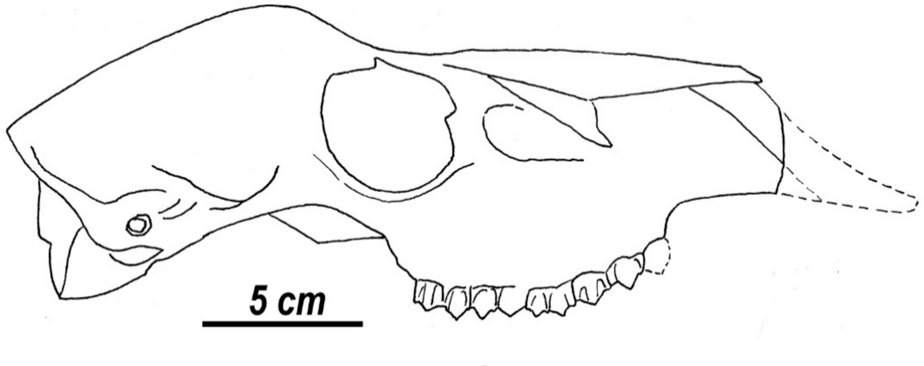

Fig. A.16. The female skull of *Metacervocerus rhenanus* (Dubois, 1904) Nr. 210638 (PMUL) from Sénèze, France

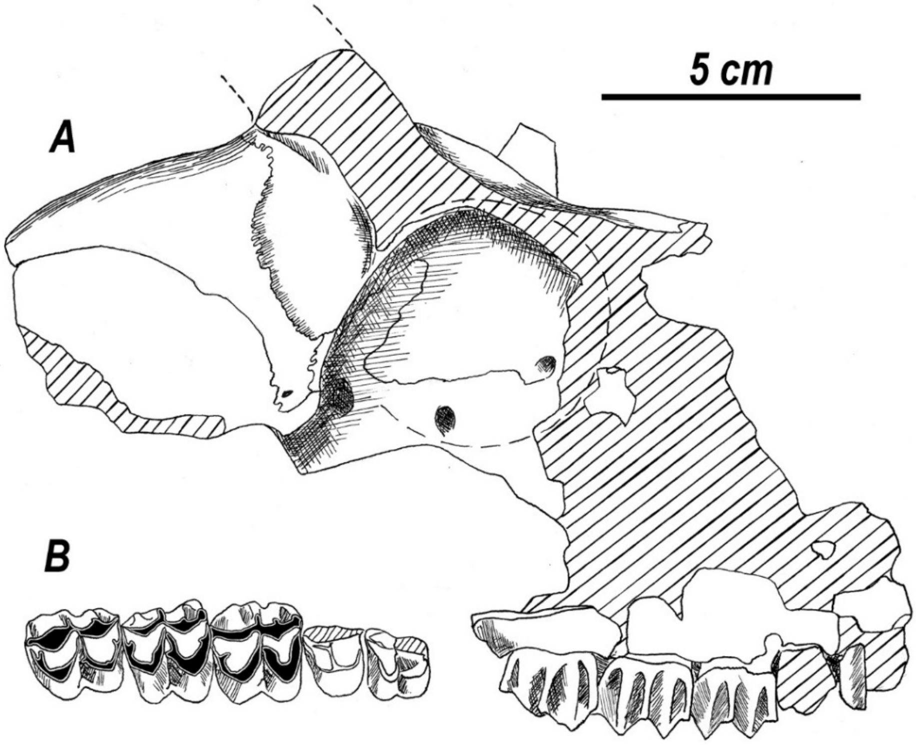

Fig. A.17. The holotype Nr. 1 (IZW) of *Praeelaphus warthae* (Czyżewska, 1968) from Węże-1, Poland: A, the side view; B, the occlusion view of right cheek tooth row

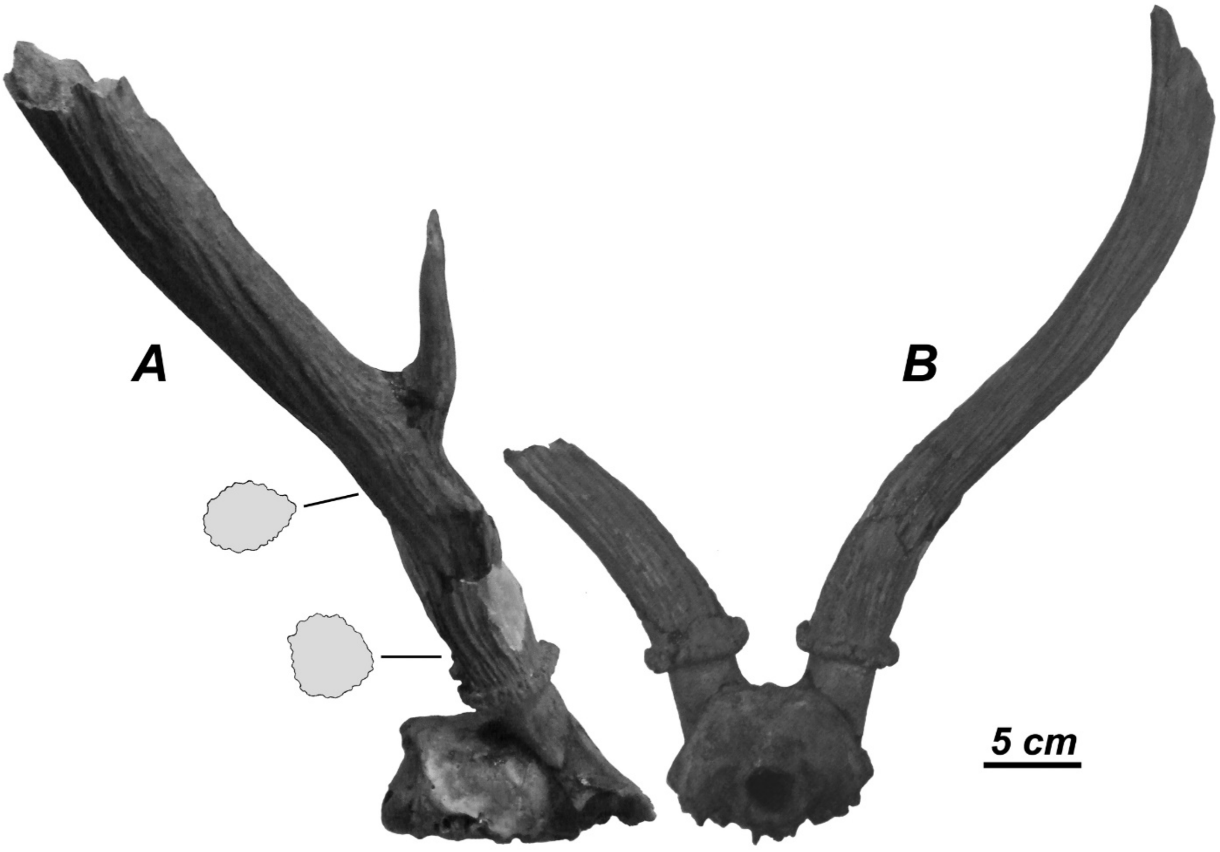

Fig. A.18. The holotype OF-24995 (NMENH) of *Praeelaphus australorienalis* Croitor, 2017 from Velikoploskoe (Ukraine): A, side view; B, occipital view

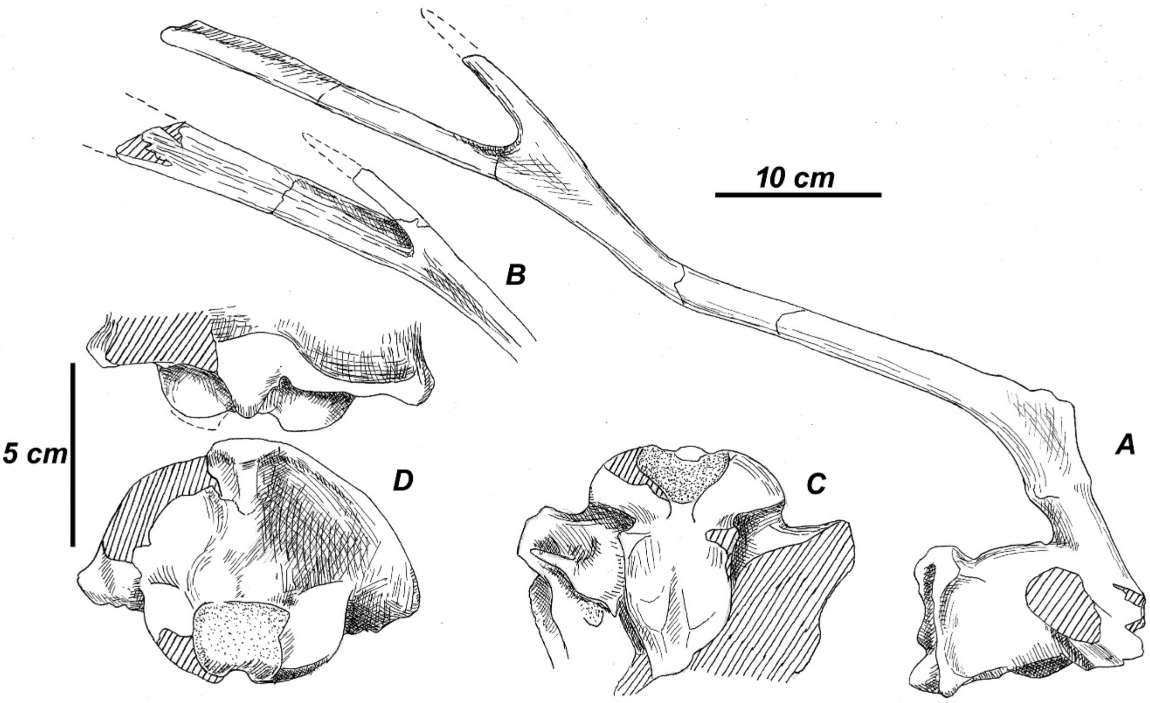

Fig. A.19. The antlered braincase IGF1378 of *Praeelaphus sp.* from Olivola, Italy: A, side view; B, anterior view of the distal part of left antler; C, upper view of the occipital profile; D, posterior view of the braincase; E, basioccipitale view of the braincase

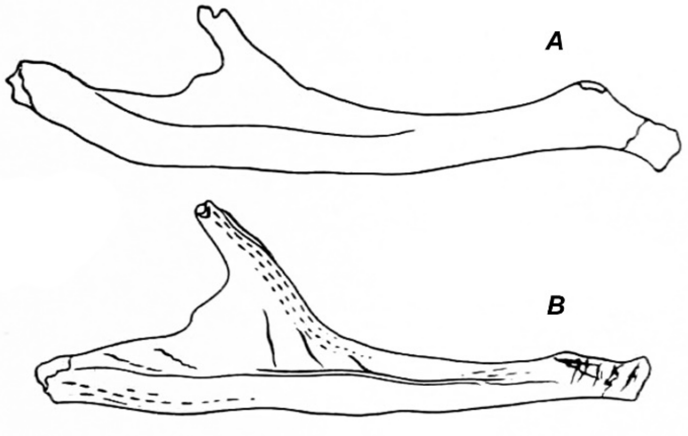

Fig. A.20. The left antler of *Praeelaphus messinae* (Pohlig, 1909) from the Pleistocene deposits of the Puntali cave (Sicily): A, medial view; B, lateral view

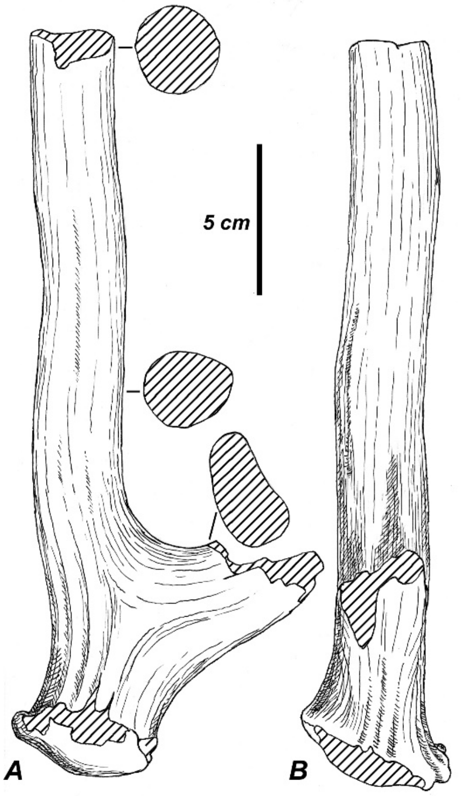

Fig. A.21. The right shed antler of *Rucervus* (*Arvernoceros*) *ardei* Croizet et Jobert, 1828 from Slobozia Mare (the Museum of Slobozia Mare, Cahul District, Moldova): A, lateral view; B, anterior view

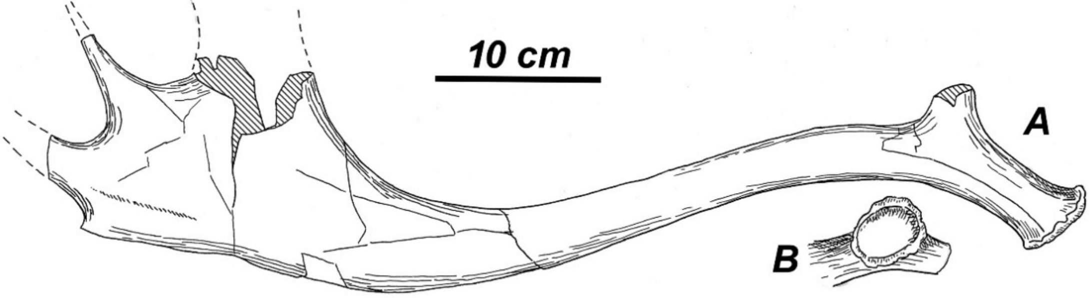

Fig. A.22. *Rucervus radulescui* sp. nov. from Valea Grăunceanului: holotype, the left shed antler "GR-965, c. 17, v. 690" (Institute of Speleology "Emil Racoviță"; ISER): (A) medial view; and, (B) basal view

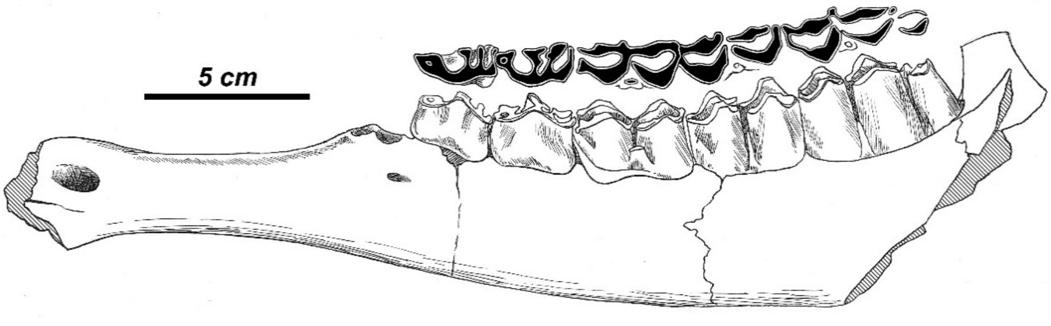

Fig. A.23. ***Rucervus gigans*** **Croitor, 2018 from Apollonia-1: the lateral view of the left mandibular ramus APL-384 (syntype; School of Geology of the University of Thessaloniki, SGUT) and the shape of the occlusal surface of toothrow**

Fig. A.24. ***Rucervus gigans*** **Croitor, 2018 from Apollonia-1: the left maxilla APL-274 (syntype; SGUT) with tooth series P^2-M^3: grinding surface view**

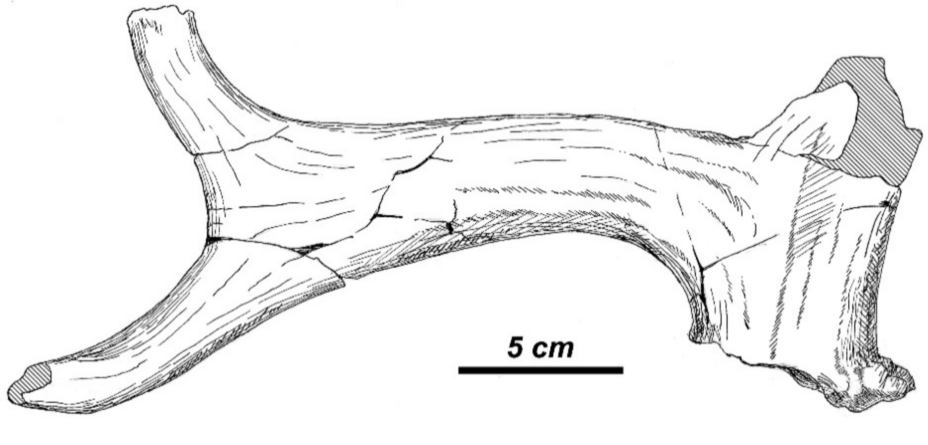

Fig. A.25. ***Rucervus gigans*** **Croitor, 2018 from Apollonia-1: the basal fragment of antler APL-357 (syntype, SGUT)**

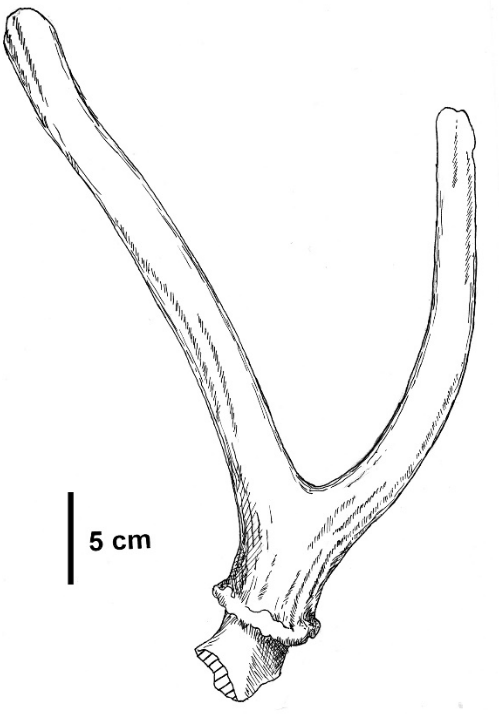

Fig. A.26. The lectotype LV-I-9-1179 of *Haploideceros mediterraneaus* (Bonifay, 1967) from Lunel-Viel (France)

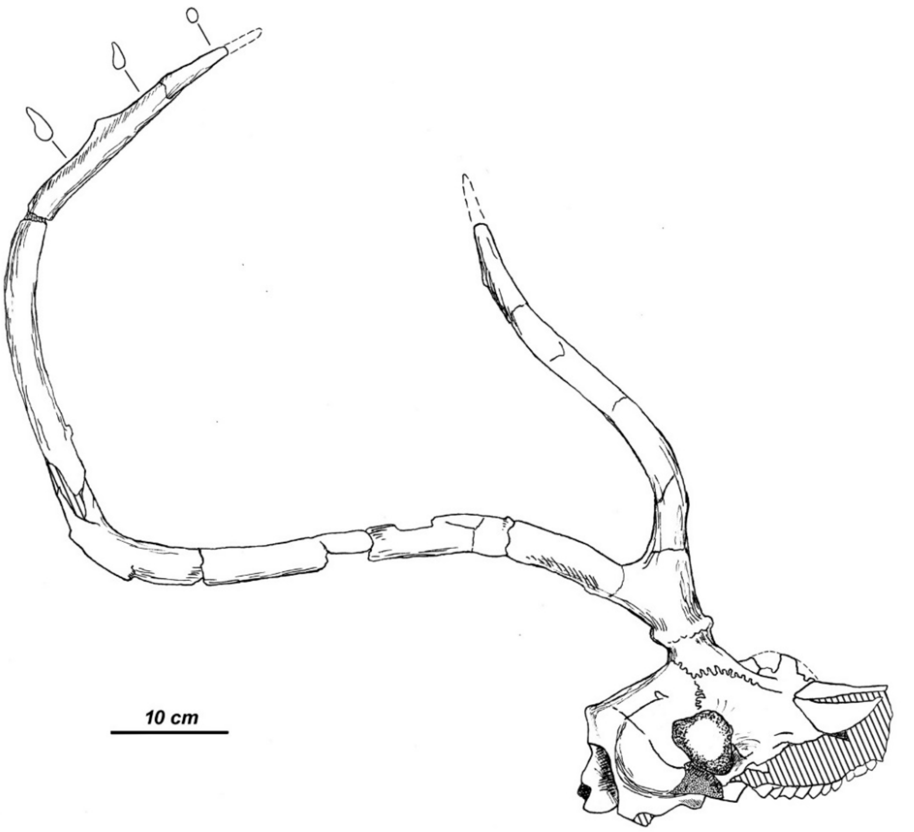

Fig. A.27. The antlered skull of *Haploideceros mediterraneaus* (Bonifay, 1967) from Cova del Rinoceront (Spain)

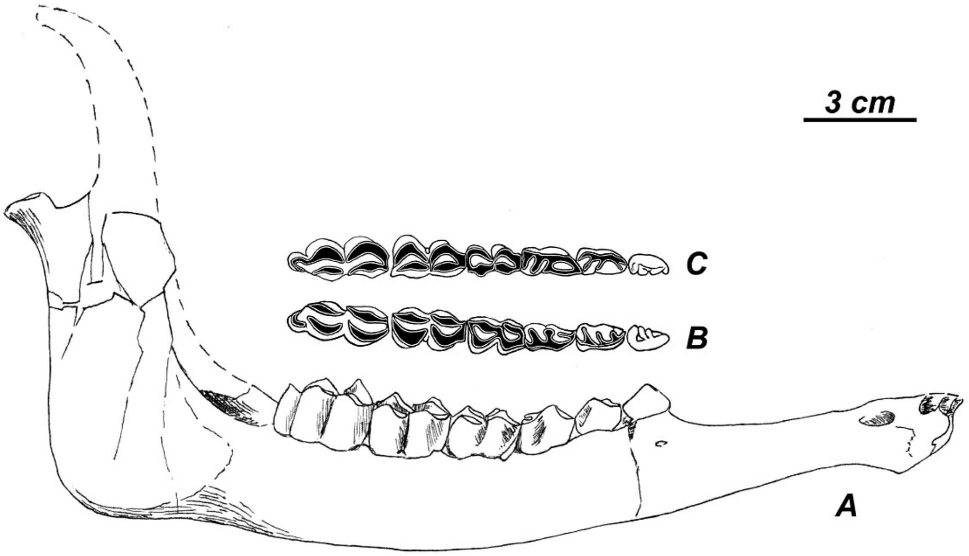

Fig. A.28. Lower mandible and lower cheek tooth rows of *Haploideceros mediterraneaus* (Bonifay, 1967) from Cova del Rinoceront (Spain)

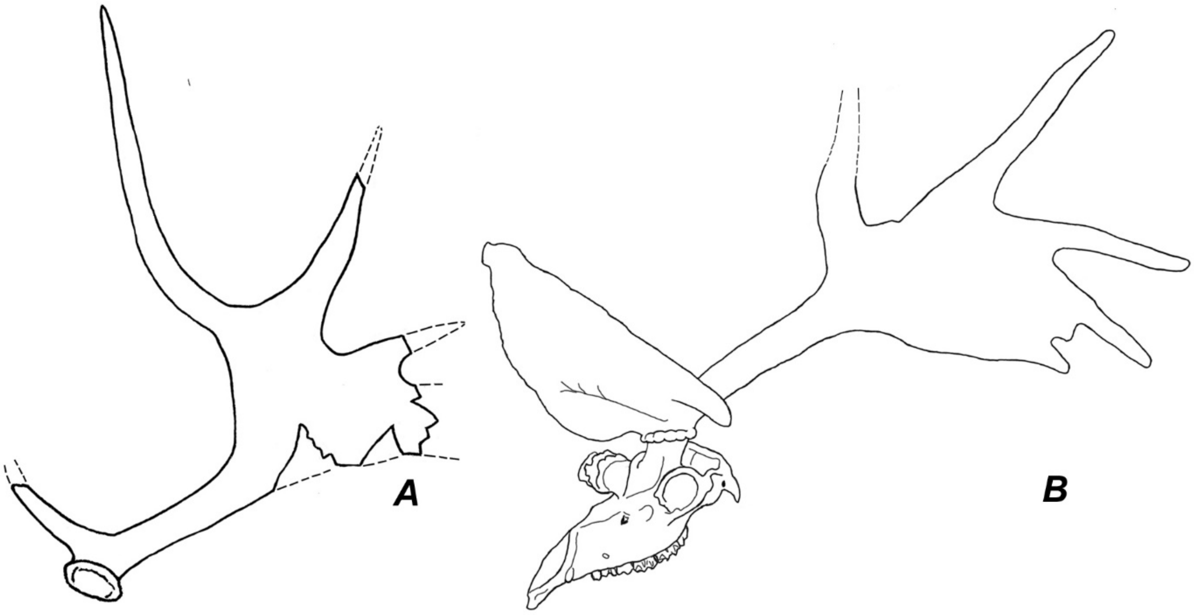

Fig. A.29. Antler shape of (A) *Sinomegaceros insolitus* (Vekua et al., 2010) from the Early Pleistocene of Dmanisi (Georgia) and (B) *Sinomegaceros pachyosteus* from the Middle Pleistocene of northern China (adapted from Teilhard de Chardin and Pei, 1941)

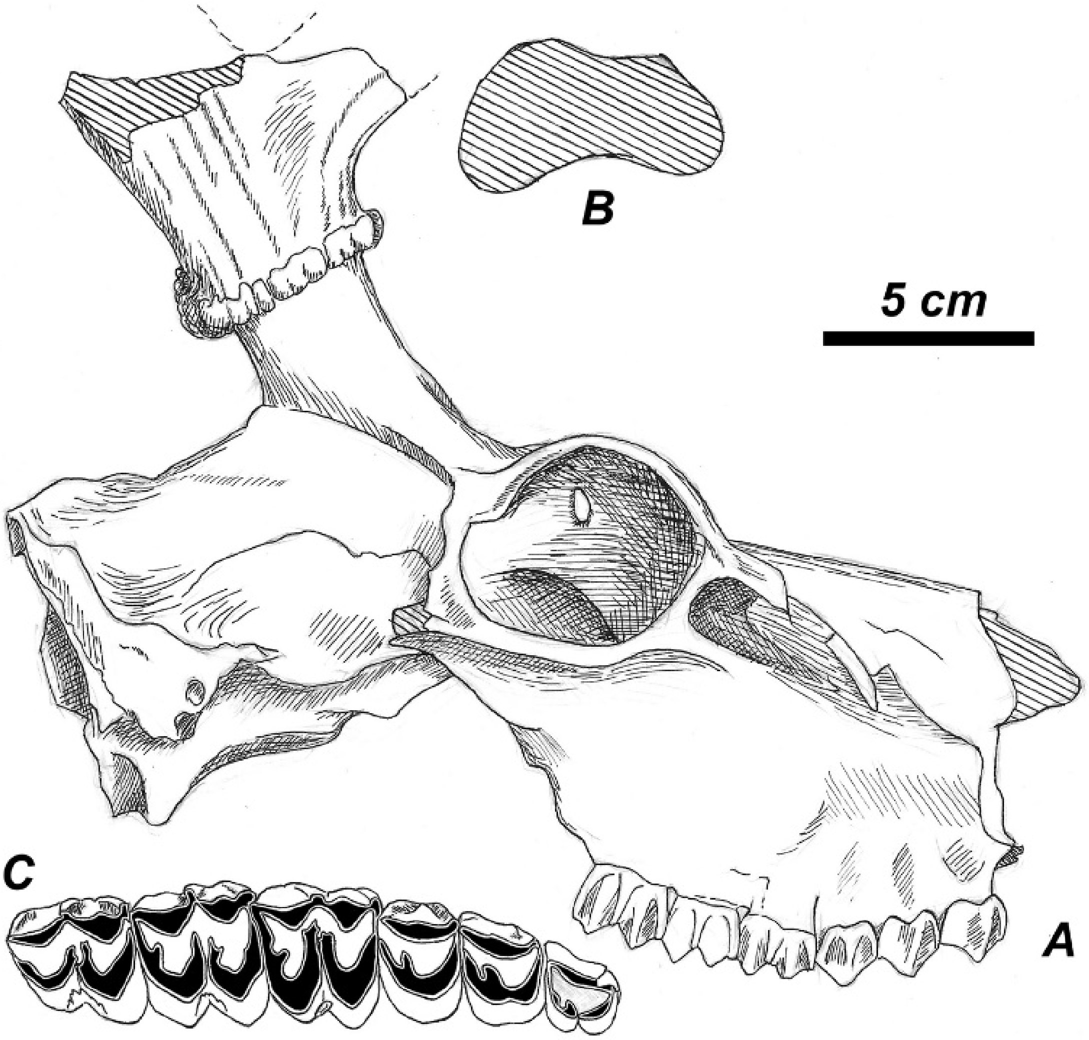

Fig. A.30. The partially preserved skull of *Eucladoceros dicranios* (Nestii, 1841) from Upper Valdarno, Italy (stored in the University of Florence): A, side view; B, cross-section of the antler below the basal ramification; C, occlusion view of the upper cheek tooth row

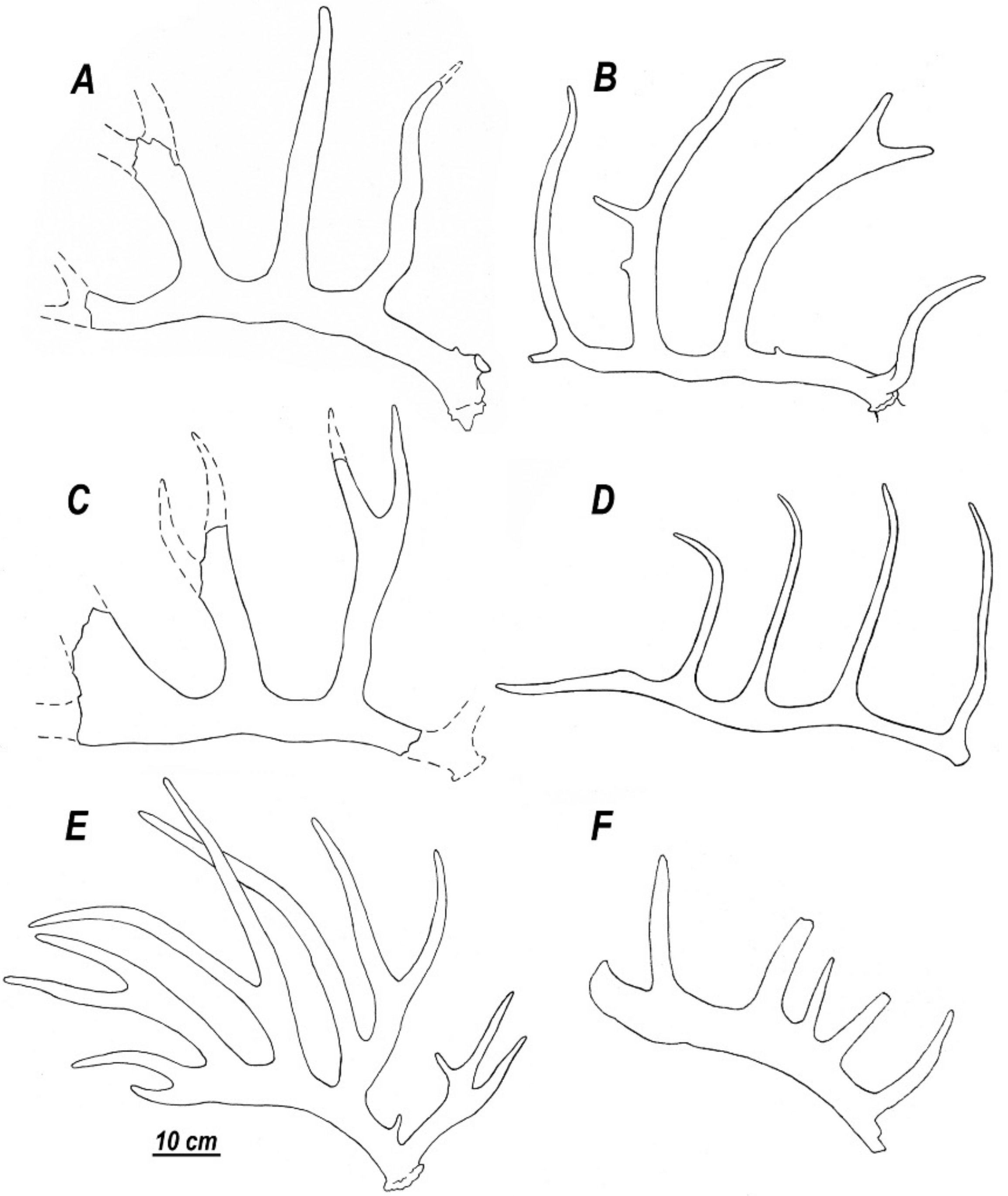

Fig. A.31. The antler shape of various forms of *Eucladoceros* from the western Palearctic: A, *E. ctenoides ctenoides* (Nesti, 1841) from Upper Valdarno, Italy (IGF377, MGUF); B, *E. ctenoides falconeri* (Dawkins, 1868) from Sénèze, France (MNHN); C, *E. ctenoides olivolanus* (Azzaroli and Mazza, 1992) from Olivola (IGF1402, MGUF); D, *E. ctenoides tetraceros* (Dawkins, 1878) from Peyrolles, France (34409, NHML); E, *E. dicranios* (Nesti, 1841) from Upper Valdarno, Italy (IGF270, MGUF); F, *E.* aff. *boulei* Teilhard de Chardin & Piveteau 1930 from Kapetanios, Greece

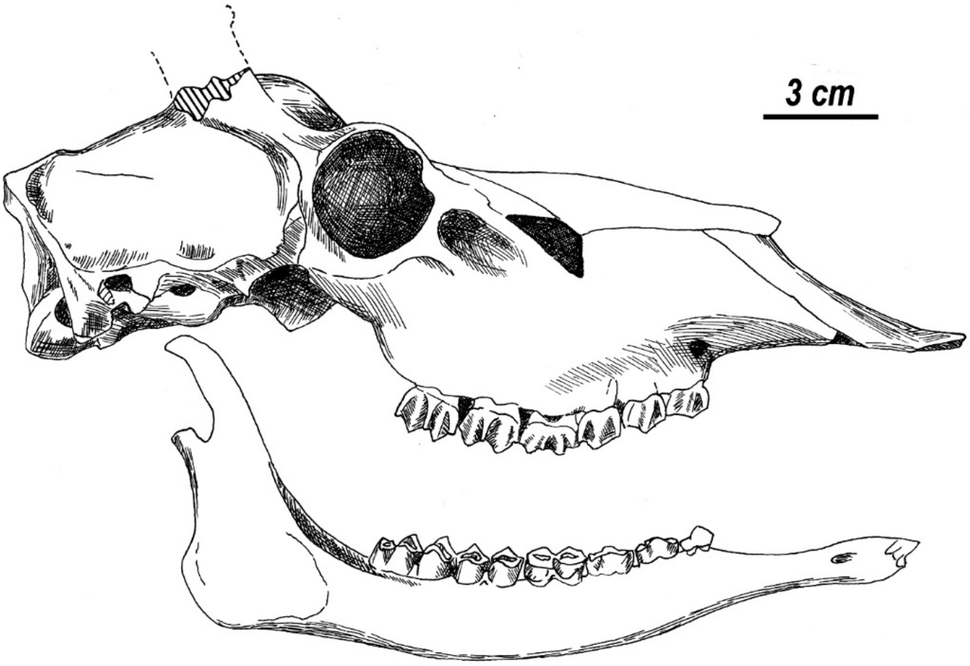

Fig. A.32. The skull of *Eucladoceros ctenoides falconeri* (= *Eucladoceros senezensis*) from Seneze. The specimen is in the paleontological exposition of the National Museum of Natural History, Paris

Fig. A.33. The shed antler of *Praemegaceros obscurus* from Salcia (Moldova): A, lateral view; B, medial view; C, upper view

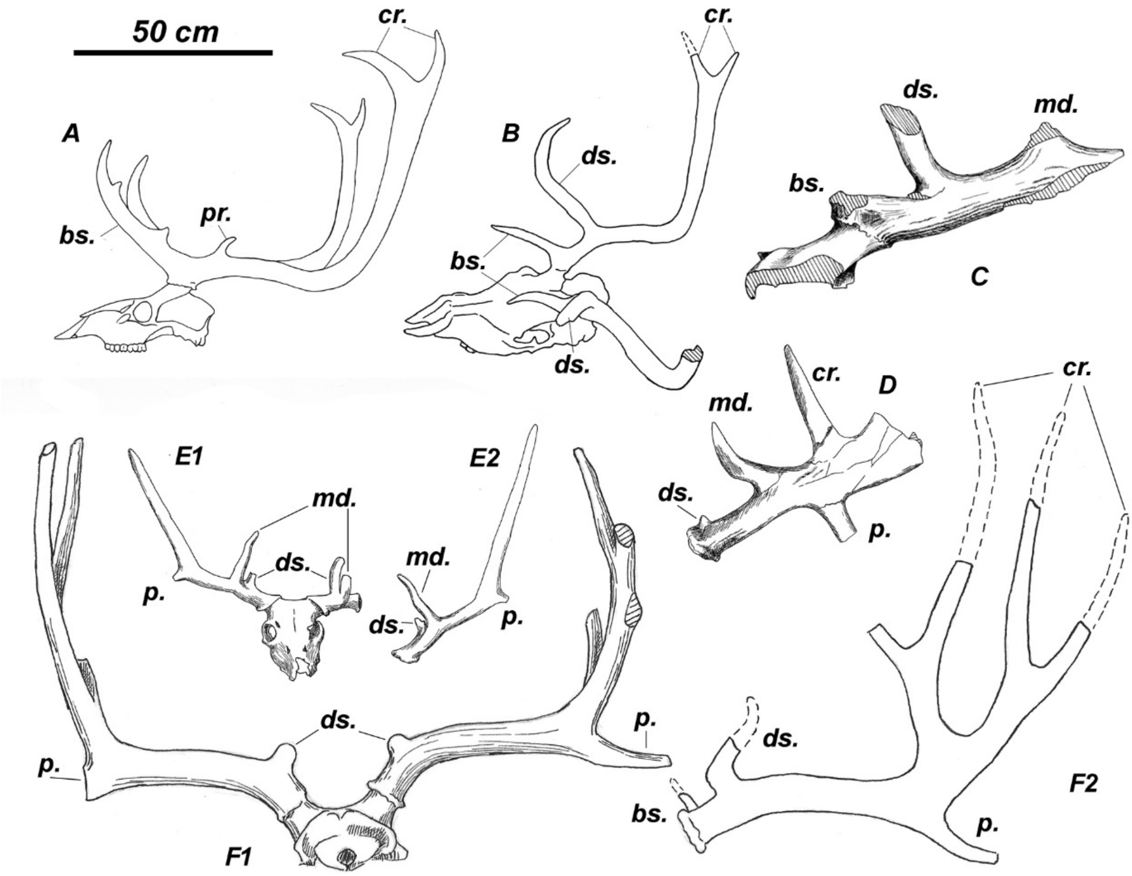

Fig. A.34. ***Praemegaceros*** **and related genera: A,** ***Panolia eldii*****; B,** ***Praemegaceros obscurus*** **from Pietrafitta, Italy (IGF 4024); C,** ***Praemegaceros obscurus*** **from Rotbav Silverstu, Romania; D,** ***Praemegaceros dawkinsi*** **from the Forest Bed Formation, England; E,** ***Candiacervus devosi*** **(adapted from van der Geer, 2018); F,** ***Praemegaceros pliotarandoides*** **from Aliakmon, Greece (adapted from Melentis, 1967). Abbreviations: bs, basal tine; ds., dorsal tine; m., middle tine; p., posterior tine; cr. crown tines**

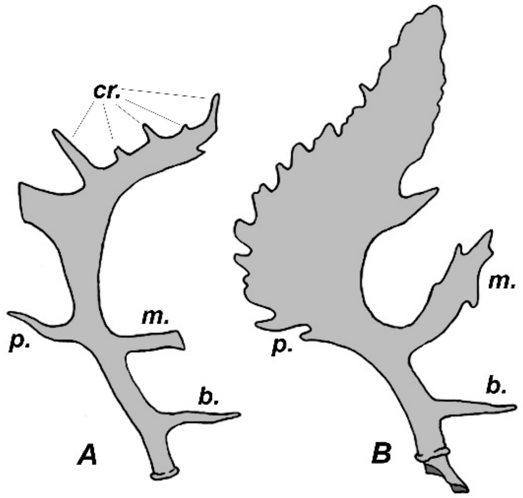

Fig. A.35. The antler vauplan of ***Praemegaceros*** **(*****Nesoleipoceros*****)** ***cazioti*** **(A) and** ***Praemegaceros*** **(*****Nesoleipoceros*****)** ***solilhacus*** **(B); abbreviations:** ***b.*****, basal tine;** ***m*****, middle tine;** ***p.*****, posterior tine;** ***cr.*****, crown tines**

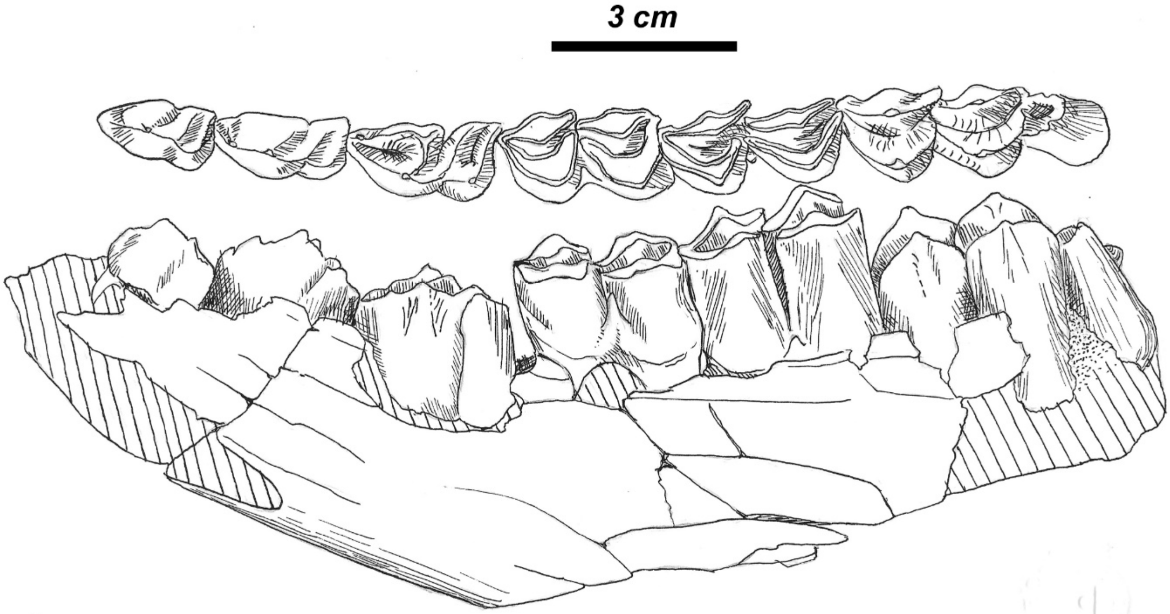

Fig. A.36. The left hemimandible APL-491 of *Praemegaceros* (*Orthogonoceros*) *pliotarandoides* (De Alessandri, 1903) from the late Early Pleistocene of Apollonia-1, Greece

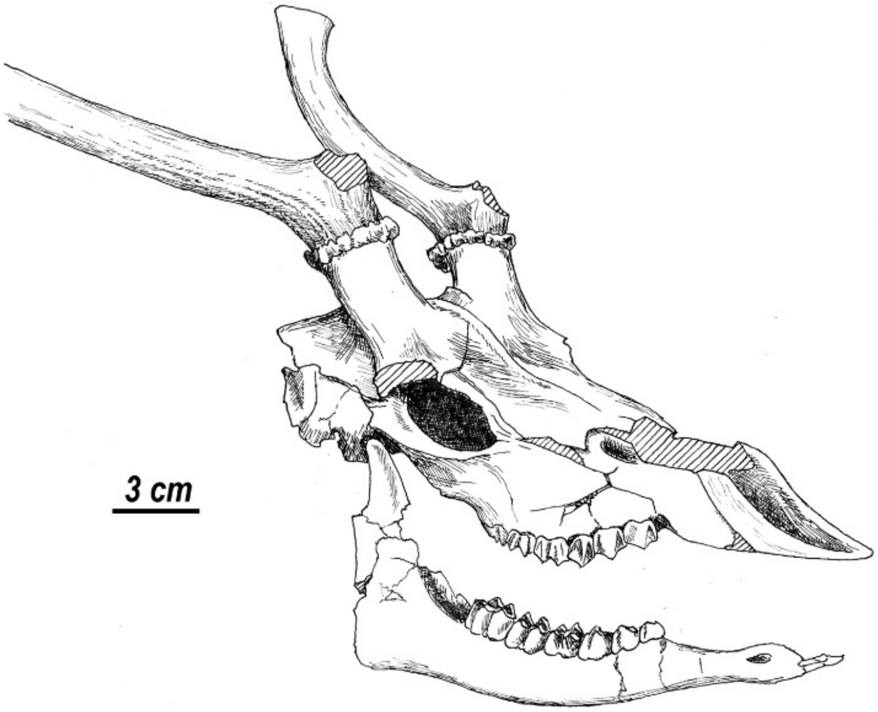

Fig. A.37. The antlered skull of a young adult male IGF 243 (MGUF) of *Cervus nestii* (Azzaroli, 1997) from Figline; oblique view

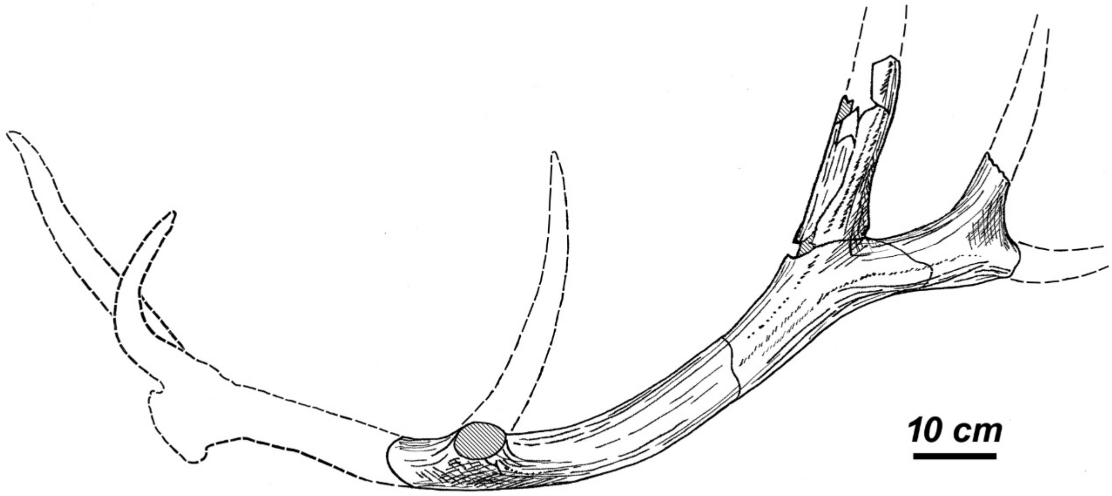

Fig. A.38. The distal fragment of antler of *Cervus canadensis* from the Paleolithic site of Climăuți (Moldova)

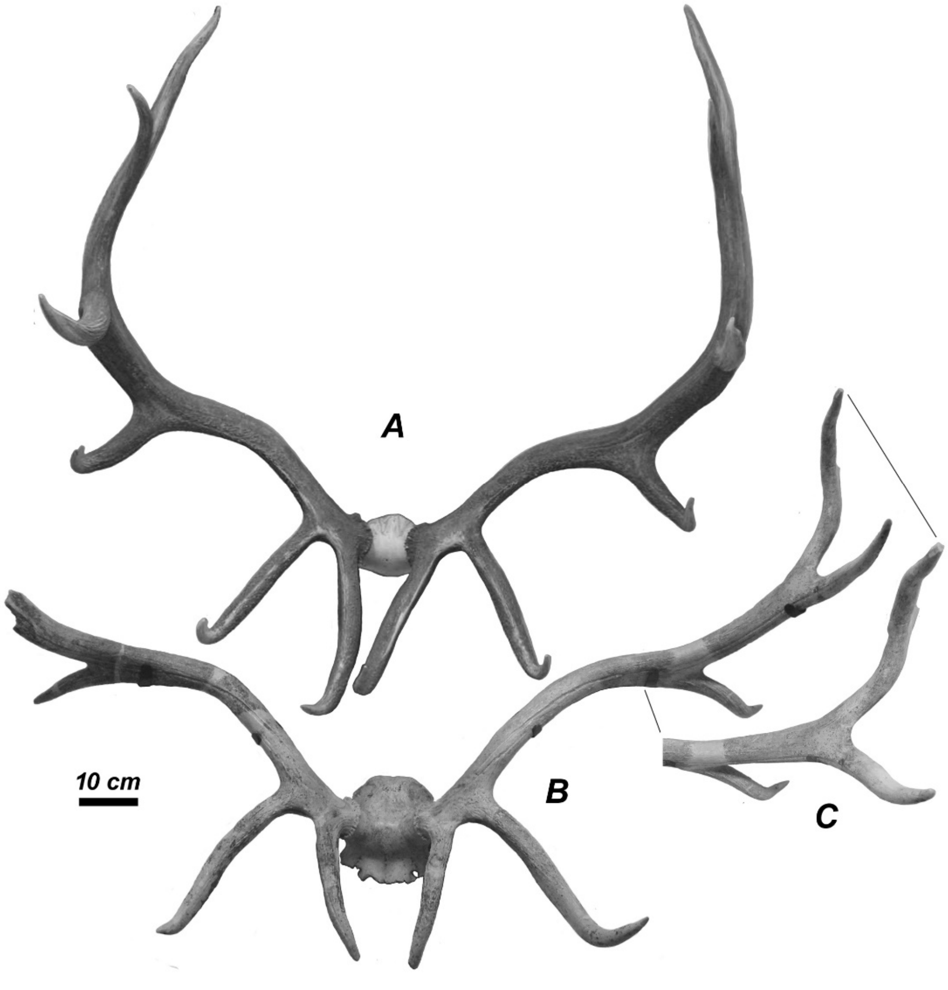

Fig. A.39. Modern and fossil subspecies of *Cervus canadensis*: A, *Cervus canadensis sibiricus*, frontal view (adapted from Stepanova and Argunov, 2016); *Cervus canadensis combtayicus*, frontal view; C, upper view of the distal portion of antler

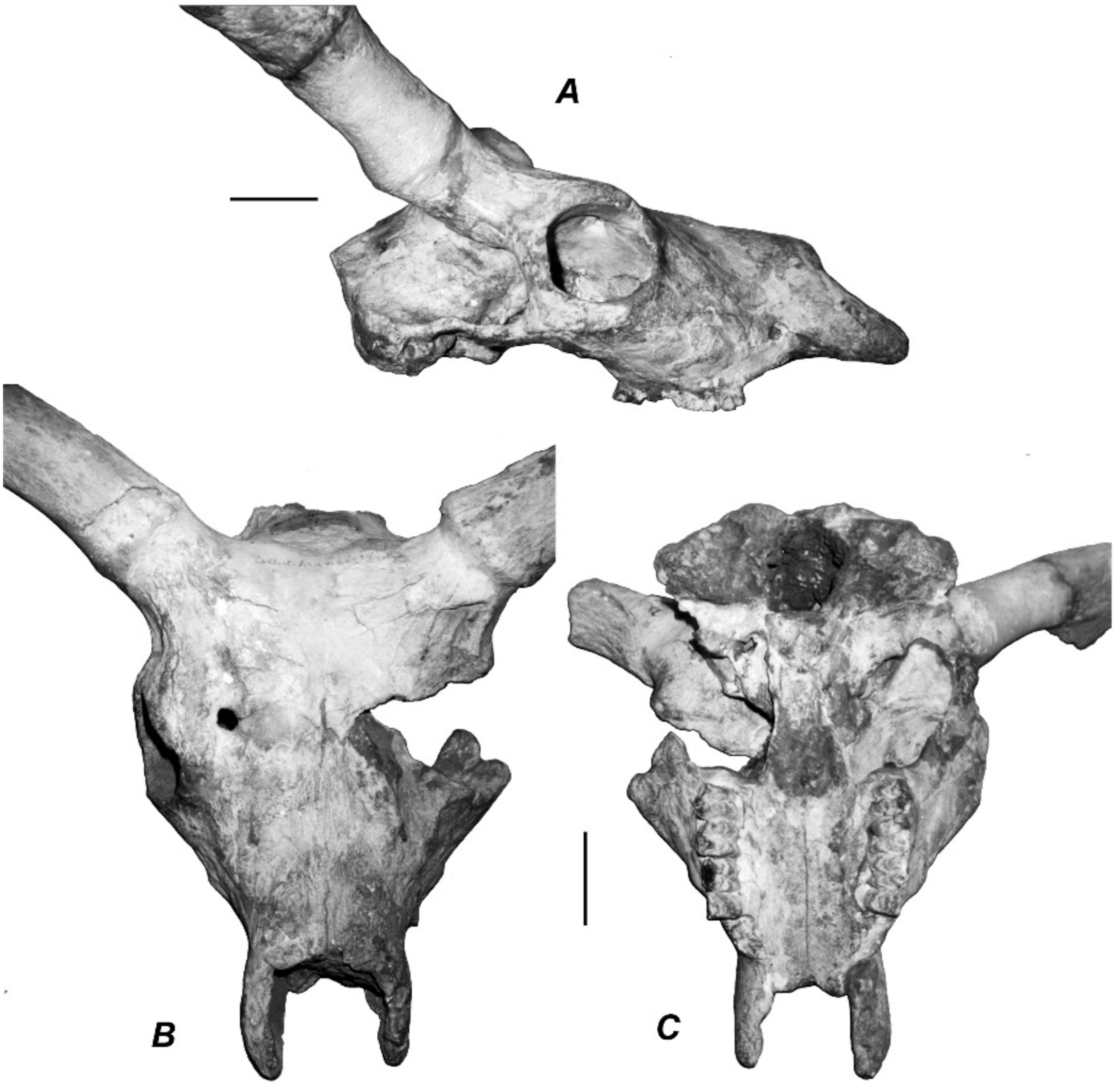

Fig. A.40. *Megaceroides algericus* **(Lydekker, 1890): the male skull from Guyotville (now Ain-Benian, Algeria) stored in Paris (NMNH, "Collection of Arambourg", no number): A, side view; B, frontal view; C, palatal view. Scale bars: 5 cm**

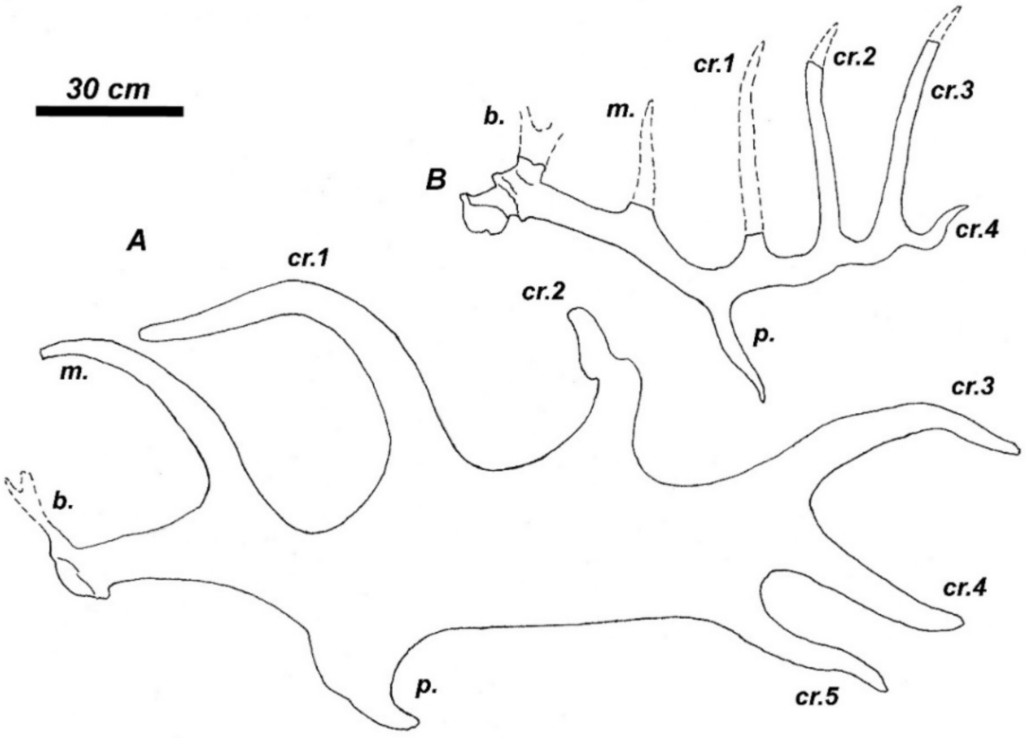

Fig. A.41. Antler bauplan of *Megaloceros* and *Praedama*: (A), *Megaloceros giganteus giganteus* from Bucharest environs, Romania (adapted from Apostol, 1976); (B) *Praedama* sp. from Pinedo, Spain (adapted from Aguado, 1962). Abbreviations: b., basal tine; m., middle tine; p., posterior tine; cr., crown tine.

DISCLAIMER OF LIABILITY

I hereby declare, under my own responsibility, that the materials presented in the doctoral thesis are the result of my own activities and achievements. I acknowledge that I will be held accountable for any violation of the legislation in force.

Roman Croitor

06.04.2023

CURRICULUM VITAE

Curriculum vitae Europass	
Personal Information	
Last name/ First Name	**Croitor Roman**
Address	Gheorghe Asachi str. 62/3, ap. 56, Chișinău, Republic of Moldova
Phone Number	+373 73-98-09 Telefon mobil: +37369345192
E-mail	roman.croitor@zoology.md
Nationality	Republic of Moldova
Date of birth	20 February 1971
Gender	male
Professional Experience	
Date	1990 - 2006
Professional position	Scientific researcher
Name and address of employer	Institute of Zoology, Academiei str. 1, MD-2028, Chișinău, Republic of Moldova
Field of work	Zoology, paleozoology
The main activities and responsibilities	Research in the field of paleozoology.

Date	2007 - 2014
Professional position	Senior Scientific Researcher
The main activities and responsibilities	Research in the field of archaeozoology.
Name and address of employer	Institute of Cultural Heritage, Ștefan Cel Mare str. 1, Chișinău, Republic of Moldova
Field of work	Zoology, arhaeozoology, palezoology
Date	2014 - prezent
Professional position	Senior Scientific Researcher
The main activities and responsibilities	Research in the field of paleozoology and archaeozoology.
Name and address of employer	Institute of Zoology, Academiei str. 1, MD-2028, Chișinău, Republic of Moldova
Field of work	Zoology, arhaeozoology, palezoology
Date	1998 - 2003
Title of qualification awarded/Level	Biologist, Biology and Chemistry teacher
Name and type of organization	State University of Moldova
Date	2003 - 2007
Title of qualification awarded/Level	Doctor in Biology
Name and type of organization	Institute of Zoology, Academy of Sciences of Moldova

Personal skills and competencies

Native language

Russian

Other languages

Romanian, English, French

Self-assessment
*CEFR**

	Understanding				Writing				Spoken	
	Listening		**Reading**		**Spoken**		**Spoken**			
English	C	Independent user	B	Independent user	B	Independent user	B	Independent user	B	Independent user
French	C	Independent user	B	Independent user	B	Independent user	B	Independent user	B	Independent user
Russian	C	Proficient user	C1	Proficient user	C	Proficient user	C	Proficient user	C	Proficient user

(*) The Common European Framework of Reference for Languages (CEFR) level

Social skills and competences

Adaptability, flexibility, communication, empathy, psychological support

Technical skills and competencies

Programming language PYTHON, SQL, Big Data, Data Analytics

Computer skills and competencies

MS Office, Excel (advanced level), Jupyter Notebook – Anaconda, PostgreSQL, Tableau, KNIME

Supplimentary information

Publications

86 scientific publications, including a monograph and a chapter in a collective monograph, 29 articles published in journals with impact factor, 14 articles in internationally recognized scientific journals, 10 articles in journals included in the National Register of specialized journals (categories A and B), 4 articles in foreign scientific collections, and 22 abstracts of scientific reports presented at 16 international conferences abroad, 4 national international conferences, as well as 3 national conferences with international participation.

Participations in scientific conferences: 30 international and national conferences.

Participations in projects: 3 institutional and international projects.

Scientific fellowships:

Natural History Museum of London, 1998 , “Systematics and Evolution of Large-sized deer”

Universita degli Studi di Firenze, 1999, “Fossil deer from Early Pleistocene of Italy”

Université de Provence, Maison Méditerranéenne des Sciences de l’Homme, Aix-en-Provence, 2001

University of Thessaloniki, School of Geology 2001, “Systematics and Paleoecology of fossil deer from Northern Greece”.

University of Greifswald, Institute of Zoology, 2002, “Ecology of Early Pleistocene fossil deer”.

University of Wroclaw, Institute of Zoology, 2003-2004, “Systematics and evolution of Pliocene deer from Eastern Europe”.

Date 12.09.2023 **Title holder,** **Croitor Roman** __________________
(name of signer, signature of title holder)

IMPLEMENTATION ACTS:

MINISTERUL CULTURII AL REPUBLICII MOLDOVA
MUZEUL NAȚIONAL DE ISTORIE A MOLDOVEI
str. 31 August 1989, 121-A, MD 2012, or. Chișinău, REPUBLICA MOLDOVA
tel. 244325, tel./fax (37322) 244369, e-mail: office@nationalmuseum.md; www.nationalmuseum.md

Nr. 149/01-06 **01.11.2022**

Act de implementare

Prin prezentul, se confirmă că rezultatele științifice obținute în cadrul tezei de doctor habilitat în științe biologice a dlui Roman Croitor intitulată ***„Cerbii din Miocenul Târziu - Pleistocenul Palearcticului de Vest: sistematica, filogenia și evoluția"***, au fost implementate în procesul determinării materialelor din colecțiile Muzeului Național de Istorie a Moldovei. Au fost prelucrate artefactele din situri paleolitice Cosăuți și Rașcov-7 confecționate din coarne, dinți și oase cerbilor din Pleistocenul superior.

Director general **dr.hab. Eugen Sava**

MINISTERUL CULTURII
AL REPUBLICII MOLDOVA

**MUZEUL NAŢIONAL
DE ETNOGRAFIE ŞI ISTORIE
NATURALĂ**

MINISTRY OF CULTURE OF
THE REPUBLIC OF MOLDOVA

**NATIONAL MUSEUM OF
ETHNOGRAPHY AND NATURAL
HISTORY**

mun. Chişinău, str. Mihai Kogălniceanu, 82; cod fiscal: 1005600000099
Tel.: (373 22) 24 40 02; Fax: (373 22) 24 40 02;
e-mail: office@muzeu.md; director@muzeu.md website: www.muzeu.md

02.11.2022 Nr. 207/01-05

ACT DE IMPLEMENTARE

Prin prezentul, se confirmă, că rezultatele ştiinţifice obţinute în cadrul tezei de doctor habilitat în ştiinţe biologice, a dlui Roman Croitor, intitulată *Cerbii din Miocenul Târziu - Pleistocenul Palearcticului de Vest: sistematica, filogenia şi evoluţia*, au fost implementate în procesul determinării materialelor din Colecţia Paleontologică a Muzeului Naţional de Etnografie şi Istorie Naturală, fiind identificată şi descrisă o specie nouă pentru ştiinţă - *Praeelaphus australorientalis* (Croitor, 2017). Holotipul speciei noi se află în Expoziţia Permanentă a Muzeului.

Datele şi rezultatele ştiinţifice obţinute în urma studierii amintitului holotip, servesc pentru completarea informaţiilor de evidenţă muzeală, de asemenea, vor servi la identificarea altor fosile preistorice din cadrul speciei identificate ca una necunoscută.

Director general **Petru VICOL**