

Historical Biology

An International Journal of Paleobiology


ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/ghbi20>


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To cite this article: Roman Croitor, Chris Robinson, Sabrina Curran, Claire Terhune, Virgil Drăgușin, Briana Pobiner, Aurelian Popescu & Alexandru Petculescu (2023): Early pleistocene ruminants (Artiodactyla, Mammalia) from the Dacian Basin (South Romania) before and after the *Pachycrocuta* event: implications for hominin dispersals in Western Eurasia, *Historical Biology*, DOI: [10.1080/08912963.2023.2167602](https://doi.org/10.1080/08912963.2023.2167602)

To link to this article: <https://doi.org/10.1080/08912963.2023.2167602>

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Early pleistocene ruminants (Artiodactyla, Mammalia) from the Dacian Basin (South Romania) before and after the *Pachycrocuta* event: implications for hominin dispersals in Western Eurasia

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ABSTRACT

The palaeontological material from the Dacian Basin provides a complete and well-represented record of faunal succession during the important faunal turnover called the *Pachycrocuta* event. The present study describes fossil remains of ruminants (Cervidae, Bovidae, Giraffidae) from the Early Pleistocene of Valea Grăunceanului, Fântâna lui Mitilan and other smaller sites from the Olteț River Valley. The article discusses the taxonomic context, eco-morphology and functional morphology of the described taxa and dynamics of biogeographic distribution. The community of ruminant species from the Dacian Basin before the *Pachycrocuta* event is dominated by Pliocene holdovers: *Pliotragus ardeus*, *Gazellospira torticornis*, *Rucervus radulescui*, *Metacervoceros rhenanus* and *Mitilanotherium inexpectatum*. This assemblage also contains new forms for Western Eurasia as *Dama eurygonos*, *Eucladoceros dicranios*, *Eucladoceros ctenoides*, *Alces* sp. and *Bison* (*Eobison*) sp. This specific regional fauna of ruminants became extinct during the *Pachycrocuta* faunal turnover and was replaced by a more cold-adapted assemblage of ruminants (*Megalovis latifrons*, *Eucladoceros* sp., *Dama* sp., *Praemegaceros obscurus* and its specialised diminished form *Praemegaceros* cf. *mosbachensis*) that show a greater affinity with coeval Levant faunas. The revealed dynamics of paleobiogeographic zones from the Early Pleistocene of southeastern Europe supports the hypothesis of early hominin dispersals in Western Eurasia via Balkan-Anatolia path.

ARTICLE HISTORY

Received 19 November 2022
Accepted 9 January 2023

KEYWORDS

Quaternary;
palaeobiogeography;
systematics; deer; bovids;
giraffids; eastern Europe

Introduction

The rich Early Pleistocene palaeontological record of the Dacian Basin is of particular paleobiogeographic interest due to its location as a cross-road between middle-latitude Asia, southern Asia, the East Mediterranean region and Central and Western Europe. Geographically, the Dacian Basin is limited by the Southern Carpathians in the North and the Balkan Mountains in the South that meet at the Iron Gates Danube Gorge in the West (Figure 1). The Dacian Basin opens eastward to the Black Sea and has readily accessible geographic connections with the Northern Black Sea plane in the East and the Aegean part of Mediterranean Sea in the South. The palaeontological material yielded by the Dacian Basin represents a practically continuous record of faunal evolution during the important continent-wide faunal and ecological transformation known as the ‘wolf event’ or ‘*Pachycrocuta* event’ (Rădulescu et al. 1998).

The term ‘wolf event’ was proposed by Azzaroli (1983) for the faunal turnover mostly based on the Western European palaeontological record and, in particular, is exemplified by the faunal transition from the Olivola to Tasso Faunal Units of the Italian Peninsula. This faunal transition chronologically lies near 1.7 Ma and was likely triggered by the climate deterioration corresponding to the Eburon cold phase (Azzaroli 1983). The ‘wolf event’ is

marked in the Italian Peninsula by the arrival of *Canis etruscus*, *Panthera onca toscana*, *Pachycrocuta brevirostris*, *Sus strozzi*, *Leptobos etruscus* and *Eucladoceros dicranios* (Azzaroli 1983; Azzaroli et al. 1986; Croitor and Popescu 2011). According to recently obtained data (Sotnikova and Rook 2010), the dispersal of wolf-like *Canis* in Asia and Europe occurred in the middle Pliocene, much earlier than has been assumed before, while *Canis etruscus* arrived in Western Europe by the end of the Pliocene (Sotnikova and Rook 2010). Martínez-Navarro (2010) proposed a more suitable term ‘*Pachycrocuta* event’ for the early Late Villafranchian faunal transformation phase, since the appearance of the giant short-faced hyena seems to have taken place practically simultaneously throughout Eurasia and Africa.

Nonetheless, the increased presence of relatively small, cooperatively hunting canids was a very important palaeoecological and palaeobiological feature of the *Pachycrocuta* event, therefore the initial evolutionary and paleobiogeographic understanding of this faunal turnover cannot be completely refuted (Sardella and Palombo 2007; Croitor and Brugal 2010). Although the *Pachycrocuta* event is mostly based on carnivoran dispersal events, it deeply affected the ecological structure and taxonomic composition of the large herbivore guilds (Brugal and Croitor 2007; Sardella

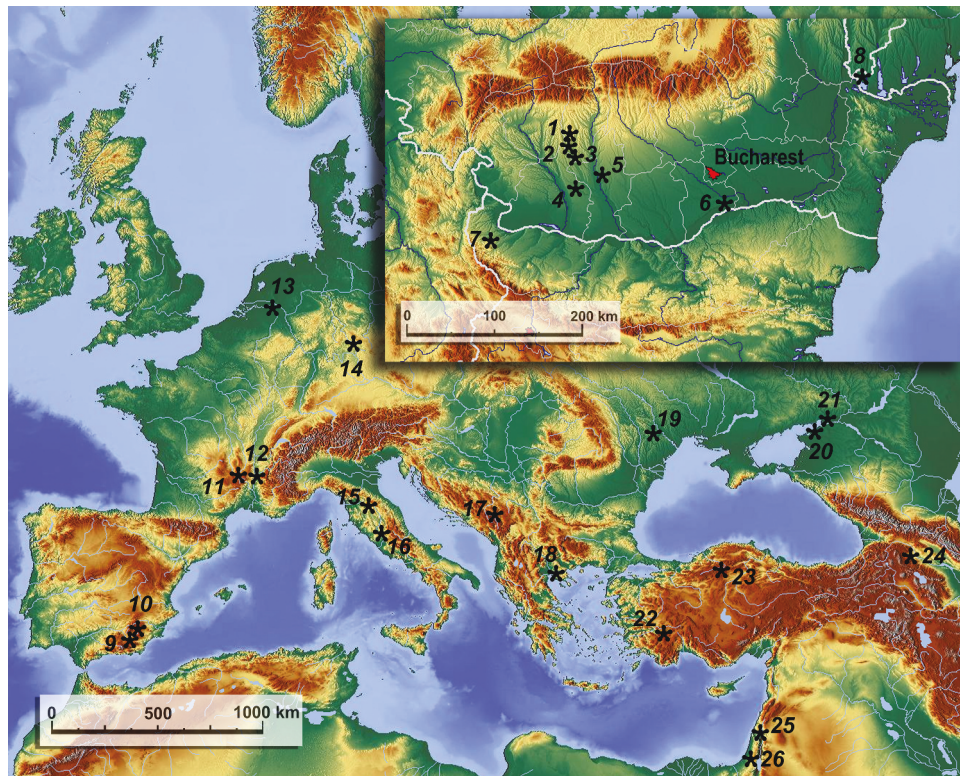


Figure 1. Geography of the Dacian Basin and geographic location of the fossiliferous sites mentioned and discussed in the present study: 1, Valea Grăunceanului; 2, La Pietriș; 3, Fântâna lui Mitilan; 4, Leu; 5, Slatina; 6, Prundu; 7, Kozarnika; 8, Dolinskoe; 9, Foneas; 10, Venta Micena; 11, Sénèze; 12, Saint-Vallier; 13, Tegelen; 14, Untermassfeld; 15, Upper Valdarno; 16, Capena; 17, Trlica; 18, Apollonia; 19, Salcia; 20, Semibalki; 21, Liventsovka; 22, Denizli; 23, Calta; 24, Dmanisi; 25, Ubeidiya; 26, Bethlehem.

and Palombo 2007). The earliest well-documented hominin presence in Western Eurasia from Dmanisi, Georgia (Lordkipanidze et al. 2007) is another important component of the *Pachyrocute* event, which sometimes is also called the *Homo* event (Leroy et al. 2011).

Faunal evolution during the *Pachyrocute-Homo* event transition in southeastern Europe is still insufficiently known, although important advancements have been made over the last few decades (Rădulescu and Samson 1990; Spassov 1997; Rădulescu et al. 1998; Spassov and Crégut-Bonnoure 1999, 2000, 2001, 2003; Rădulescu 2005; Sirakov et al. 2010, 2016; Strait et al. 2016; Lopatin et al. 2019). Our recent preliminary report revising the Early Pleistocene palaeontological material from the Olteț River Valley (Romania) allowed clarification of the biochronologic framework and updated the faunal lists, providing better understanding of Early Pleistocene faunal evolution in the Dacian Basin (Terhune et al. 2020). Relatively stenobiontous and sensitive to floral conditions, ruminant communities represent a quite accurate proxy for paleobiomes and palaeoecological conditions and serve as a useful paleobiogeographic tool (Janis 1976; Köhler 1993; Solounias and Moellken 1993, 1999; Curran et al. 2021).

The rich palaeontological record from the northwest of the Dacian Basin provides a continuous archive of the development of Early Pleistocene mammalian faunas that reveal faunal evolution in the well-defined zone between the Southern Carpathians and the Balkan Mountains (Rădulescu and Samson 1986, 1990; Popescu 2004; Rădulescu 2005). The mammalian fossil material from the Early Pleistocene deposits of the Olteț River Valley (ORV) in Southern Romania is particularly rich and offers the most complete Early Pleistocene palaeontological record from southeastern Europe revealing faunal successions during the 40-kyr glacial-interglacial cycles (Rădulescu and Samson 1990; Andreescu et al. 2011;

Terhune et al. 2020). The primarily sandy-pebbly facies of ORV are described as the Tetoiu Formation (Rădulescu and Samson 1990). More than a dozen fossiliferous sites from the Olteț River Valley in Vâlcea County are located between Tetoiu (former Bugiulești) in the north and Irimești in the south ((Rădulescu 2005), Figure 1; (Terhune et al. 2020), Figure 2). The fossiliferous sediments are of fluvial and deltaic origin and include several cycles of deposition that seem to be determined by climatic oscillations (Rădulescu and Samson 1990; Andreescu et al. 2011; Curran et al. 2021). The deltaic and fluvio-lacustrine origin of deposits is related to the presence of Dacian Lake, which was interconnected with the Pannonian and Euxinic lakes to the northwest and east, respectively (Andreescu 2009; Andreescu et al. 2013; Terhune et al. 2021). The yielded mammalian faunas cover the time span from 2.588 Ma to ca. 1 Ma (Rădulescu and Samson 1990; Andreescu et al. 2011; Terhune et al. 2020, 2021). The most important fossiliferous sites that yielded the rich material of ruminants studied in the present paper are Valea Grăunceanului (= Grăunceanu), La Pietriș and Fântâna lui Mitilan.

The composition of the mammalian assemblage from Grăunceanu indicates a geological age between 2.2 and 1.8 Ma and shows similarity with faunas from Saint-Vallier and Senèze (France), Khapry (south of European Russia) and the Costa San Giacomo and Olivola Faunal Units (Terhune et al. 2020). However, the fauna of Grăunceanu also contains peculiar mammalian species such as a new species of pangolin ascribed to the African genus *Smutsia*, *S. olteniensis* (Terhune et al. 2021) and the unusual combination of such species as *Paradolichopithecus arvernensis*, *Pachystrutio* cf. *pannonicus* and *Canis etruscus* (Terhune et al. 2020). The fauna from La Pietriș is less diverse; however, the available data suggest similarities to the Grăunceanu biostratigraphic position (Rădulescu and Samson 1990; Terhune et al. 2020). Two faunal horizons outcrop at the site of Fântâna lui

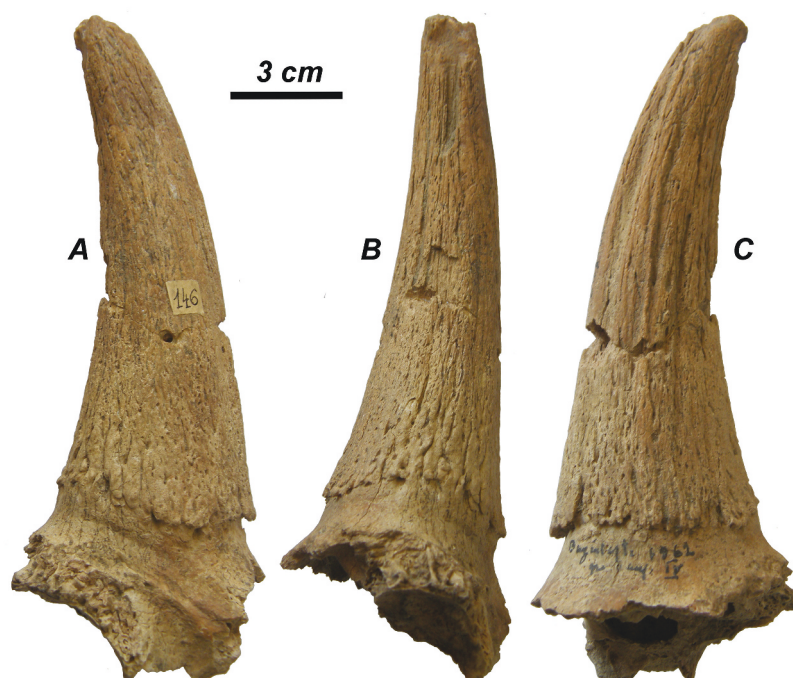


Figure 2. Horn core of *Pliotragus ardeus* from Valea Grăunceanului: A, lateral view; B, posterior view; C, medial view.

Mitilan: the main lower fossil bed is approximately dated to 1.6 Ma, while the upper faunal level is likely ca. 1.1 Ma or younger (Terhune et al. 2020). The faunas from the considered fossiliferous sites are dominated by ruminants, which are exceptionally diverse in species and represented by rich samples of skeletal remains.

Our article is focused upon taxonomic issues, evolutionary history, biogeographic origins and paleobiogeographic contexts of the Early Pleistocene ruminant herbivores that mostly come from the Olteț River Valley of the Dacian Basin. Ultimately, we aim to reveal the evolutionary and ecological transformations of the local ruminant communities, as well as paleobiogeographic evolution in the entire Dacic Basin.

Material and research methods

The main part of the studied material of fossil ruminant species (Bovidae, Cervidae and Giraffidae) from the Olteț River Valley (Valea Grăunceanului, Fântâna lui Mitilan, La Pietriș, Slatina, Slatina-2, La Baltini) is stored in the Institute of Speleology ‘Emil Racoviță’ of the Romanian Academy of Sciences, Bucharest and in the Museum of Oltenia, Craiova, Romania. The fossil material includes all skeletal parts (cranial remains, cranial appendages, post-cranial elements, tooth series and isolated teeth) at different stages of preservation, including complete or nearly complete limb bones, mandibles, horn cores and antlers.

The comparative material includes samples of cervid and bovid forms from Sènèze, France (stored in the Palaeontological Museum of Claude Bernard University of Lyon 1 and the National Museum of Natural History in Paris); Chilhac, France (the Palaeontological Museum of Chilhac); the Cromer Forest Bed Formation, England (the Natural History Museum of London) and Upper Valdarno, Italy (the Museum of Geology and Palaeontology of the University of Florence). Our comparative study is based on the original data collected earlier by one of the authors (RC).

The dental morphology terminology is applied from Heintz (1970) and Janis and Scott (1987). The measurements are taken according to the recommendations of Driesch (1976). The height of first antler ramification is measured from the medial side. The cheek tooth row length or length of the tooth series in cervids and bovids is measured as a maximum length at the tooth crowns. The tooth crown length is measured at the occlusal surface; the tooth crown breadth is taken as a maximum linguolabial measurement. The angle between the lingual rib of the protocone and the mesostyle of the paracone on M^2 is measured according to the scheme proposed by Croitor (2016a). An estimated body mass of ruminant species is provided based on dental variables according to the method proposed by Janis (1990).

The paleobiogeographic analysis is based on the multivariate cluster analysis of the regional assemblages of ruminants. The hierarchical clustering paired group algorithm UPGMA was computed using Jaccard Similarity Index for presence-absence data (PAST-3 application: Hammer et al. 2001). The cophenetic correlation coefficient is computed in order to estimate how faithfully a dendrogram preserves the pairwise distances among the original, unmodeled data points (Farris 1969). Western Eurasia was divided into paleobiogeographic areas corresponding to the geographically delimited zones that yielded characteristic and taxonomically rich herbivores faunas (Croitor 2018a). Coeval faunas of Tajikistan (‘Central Asia’) are included in the study in order to estimate the importance of Asian biogeographic components in the paleobiogeographic areas of Western Eurasia (supplementary materials, Tables S1 and S2). The faunas involved in the analysis correspond to the stages of biogeographic evolution termed as ‘Saint-Vallier Age’ and ‘Untermassfeld Age’ (Croitor 2018a). The analysed faunal lists are built using conservative taxonomical criteria: only species and groups of closely related species are considered (subspecies and local mammal forms are not taken in account). A group of species

or morphological forms are regarded as a single faunal element if they are proved to have a direct phylogenetic relationship or if they are distinguished only by body size or minor morphological variants of exosomatic structures (Croitor 2018a).

Abbreviations used in the article: DLM, mediolateral diameter; DAP, anteroposterior diameter; L, length; H, height; D, breadth; CFR, circumference; dist, distal; prox, proximal; diaph, diaphysis; ap., apical part of antler beam; bs., basal tine of antler; cr., crown tine of antler; VGr, Valea Grăunceanului; FM, Fântâna lui Mitilan; ISER, Institute of Speleology 'Emil Racoviță'; MO, the Museum of Oltenia, Craiova; NHML, the Natural History Museum of London.

Systematic palaeontology

Family Bovidae Gray, 1821

Subfamily Caprinae Gill, 1872

Tribe Rupicaprini Simpson 1945

Genus *Pliotragus* Kretzoi, 1941

Pliotragus ardeus (Depéret, 1884)

Site

Valea Grăunceanului (= Grăunceanu).

Horn cores

The horn cores are rather short, cone-shaped, gently curved and a little compressed from the sides (Figure 2). Thus, the horn-core cross-section is oval as in the type specimen from Perrier-Etouvaires (Depéret 1884). The proximal parts of the horn cores and frontal bones are pneumatized. The horn-cores of *P. ardeus* from VGr are quite large and robust if compared to the samples of *Soergelia* from Venta Micena and Dmanisi described by Martínez-Navarro et al. (2012). The stronger horn-core compression is another important feature that distinguishes the small-sized Iberian and Caucasian Early Pleistocene *Soergelia* from *Pliotragus ardeus*: the index of horn-core compression (maximum/minimum horn-core base diameter) in *Soergelia* cf. *minor* from Dmanisi is 63.5% and 69.6%. In the sample of *Soergelia minor* from Venta Micena, the index of compression varies from 70.3% to 79.0% ($M = 74.1\%$; $n = 10$; Martínez-Navarro et al. 2012). In *P. ardeus* from VGr, the index of horn-core compression varies between 78.9% and 98.5% ($M = 91.3\%$; $n = 5$) (Table 1).

The range of size variation of the horn-core sample from VGr is significant compared to other samples involved in the comparative study (Figure 3). Such a broad range of size variation indicates the presence of well-expressed sexual dimorphism and proves the development of horn cores in females of *P. ardeus*. According to the available data, sexual dimorphism influenced only horn-core size, not the degree of horn-core compression. Therefore, the holotype of *P. ardeus* from Sénèze, according to the basal diameter (45 mm) reported by Depéret (1884), belongs to a female. The two largest specimens (VGr.1989 and VGr.454/207) we define as male horn cores, while six other smaller specimens are reported here as female (Table 1). The male horn cores are as large as the horn core of *Soergelia elisabethae* from Süssenborn. It is necessary to mention that the size of the horn core of *Soergelia* cf. *minor* from Monte Argentario, Italy (Martínez-Navarro et al. 2012) and its low degree of compression approaches that of the female horn cores from Valea Grăunceanului.

Mandible

The well-preserved mandible VGr.1465 retains both hemimandibles, though it lacks small anterior parts with the canines and

incisor teeth, the coronoid processes, and both left and right P_2 . The angle between the horizontal mandibular body and the ascending ramus (measured along the alveolar row and the median line of the ascending part) is 100° . The processus angularis is well expressed. The lower margin of mandibular body is convex with its maximum height under M_3 . There is a well-marked incision between the lower border of the dental portion of the mandibular body and the processus angularis. The mandible from VGr is roughly the same size as the mandible FSL-5008 of *Gallogoral meneghinii* from Sénèze (Figure 4). Nonetheless, the mandibles of *P. ardeus* and *G. meneghinii* are clearly distinguished by their shape and proportions. Unlike *G. meneghinii*, the mandible from VGr is characterised by a narrower angle between the horizontal and ascending parts (ca. 110° in *G. meneghinii*), an absolutely and relatively longer diastema and a relatively higher mandibular body under P_2 that then becomes relatively and absolutely shallower under M_1 (Table 2). Compared to *Megalovis latifrons*, the mandible from VGr is characterised by the relatively and absolutely longer distance between the M_3 and the posterior edge of processus angularis. Generally, the mandible of *Pliotragus* from VGr is distinguished from *Megalovis* and *Gallogoral* by an elongated horizontal ramus with relatively long premolars and a long diastema.

Dentition

The lower premolar series of the mandible VGr.1465 is relatively long (P_2P_4/M_1M_3 ratio = 59.6%) and differs from the short premolar series of *Soergelia* from Süssenborn, Bad Frankenhausen, Apollonia-1 and Venta Micena that show a rather compact range of variation of the relative length of the lower premolars. According to Crégut-Bonnoure and Dmitrijevic (2006), the premolar/molar ratio (P_2P_4/M_1M_3) in *Soergelia* ranges between 46.7% and 55.5%. The lower premolar series in the mandible from VGr is slightly longer than in the specimen from Trlica (P_2P_4/M_1M_3 , 57.1%) described by Crégut-Bonnoure and Dmitrijevic (2006) as *Soergelia intermedia*, which is characterised by a slightly shorter premolar series.

The measurements of the lower cheek teeth are quite close to those of *P. ardeus* from Sénèze, but the Romanian form is characterised by somewhat shorter premolar crowns (Figure 5) that could be related to a more advanced degree of tooth wear. The morphology of the lower fourth premolar in the specimen from VGr generally corresponds to the shape of P_4 of *P. ardeus* from Sénèze (Duvernois and Guerin 1989) (Figure 3), with the exception of the relatively larger posterior lobe of P_4 (Figure 6). Premolars of *P. ardeus* from VGr are relatively longer if compared to those of *Soergelia* sp. described by Vekua (1995) from Dmanisi (Figure 5). Crowns of lower cheek teeth in *P. ardeus* from VGr are generally shorter than in *Soergelia* (Figure 5).

A small ectostylid on M_1 of the mandible VGr.1465 is a potentially important diagnostic character that distinguishes *Pliotragus* from most of the Caprinae genera (Figure 6). The development of basal pillars is not common in Caprinae and is reported only in a few genera grouped in the tribe Ovibovini, including also the modern genus *Ovibos* (Sokolov 1953; Duvernois and Guerin 1989; Spassov 2006). The shape of the third lobe on M_3 is another important morphological feature. Duvernois and Guerin (1989) regarded a pinched third lobe with a concave lingual wall on M_3 as a diagnostic character of *Pliotragus*. However, the specimen VGr.1465 shows that this character is extremely variable and may show a different condition even in the same individual: the left M_3 is characterised by a pinched third lobe with a sharpened posterior end and a slightly concave lingual wall. However, the right M_3 third lobe is rounded and its lingual wall is rather convex (Figure 6).

Table 1. *Pliotragus ardeus* from Valea Grăunceanului: horn core measurements. Data on GR-454/207 and GR-393 are adapted from Bolomei (1965).

Measurements	VGr-1931, ♀	VGr-0929, ♀	VGr-2136, ♀	VGr-1937, ♀	VGr-1415, ♀	VGr-1989, ♂	GR-454/207, ♂	GR-393, ♀
D max pedicle	47.4			50.9	54.0	83.3		
D min pedicle	43.0	42.7		49.0	47.0	65.0		
D max horn core	48.3			52.0		91.2	67.0	56.0
D. min horn core	46.5	44.0		45.0		72.0	66.0	54.0
L horn core	140.0	>140.0	>140.0				190.0	
CFR horn core	152.0		176.0	158.0		263.0	211.0	175.0

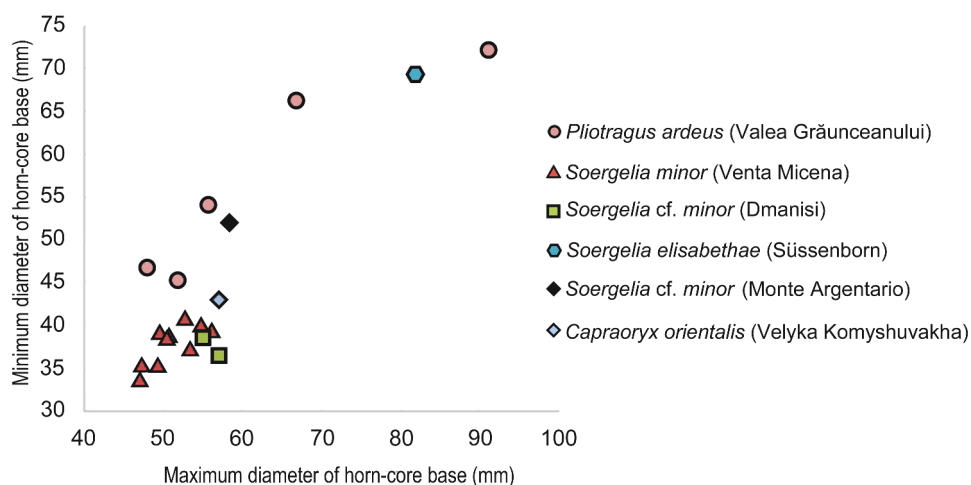
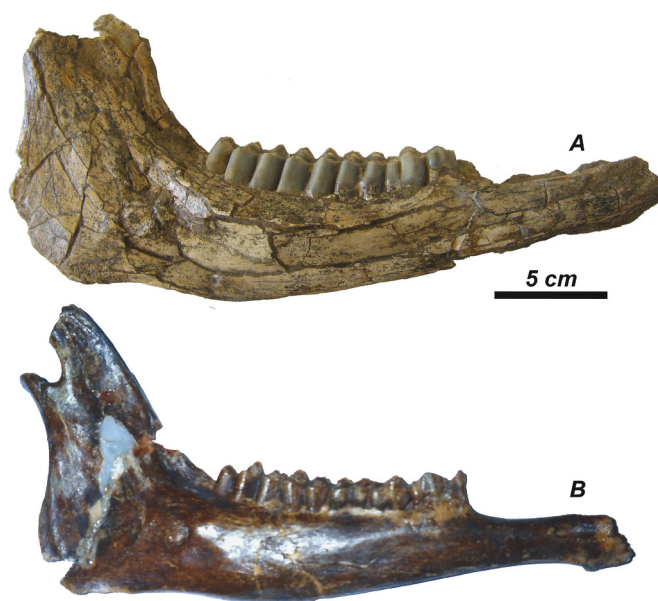
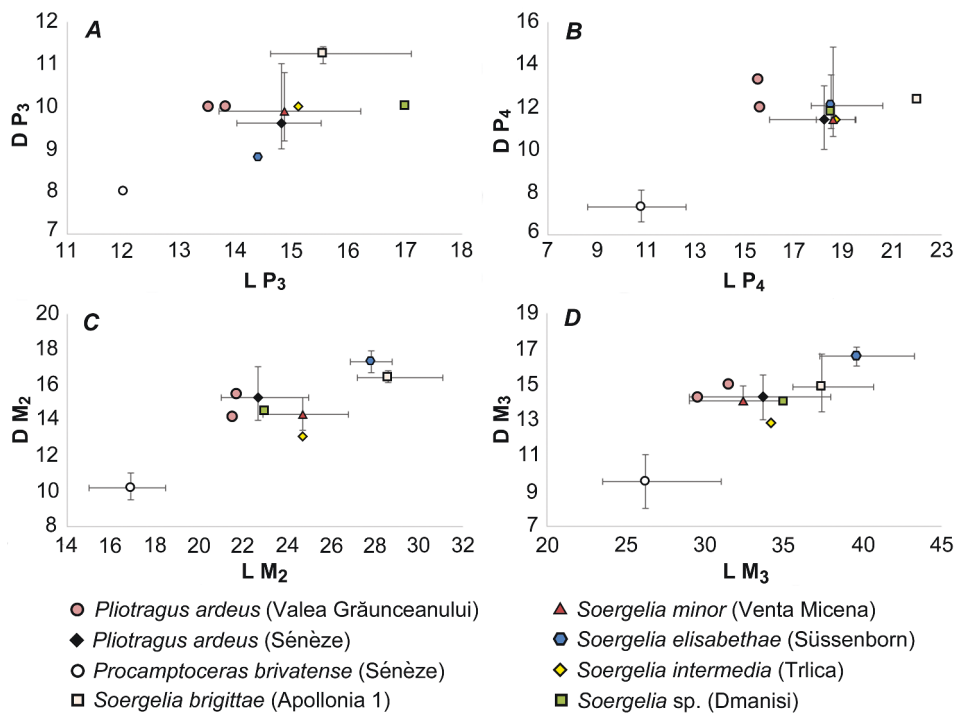
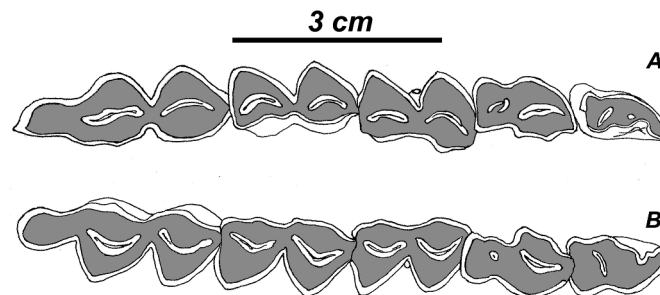
**Figure 3.** Scatter diagram of horn-core base diameters of *Pliotragus ardeus* from Valea Grăunceanului compared to the samples and specimens of Early Pleistocene Caprinae: *Soergelia cf. minor* from Dmanisi, *Soergelia cf. minor* from Monte Argentario, *Soergelia minor* from Venta Micena, *Soergelia elisabethae* from Süssenborn (all data are adapted from Martínez-Navarro et al. 2012) and *Capraoryx orientalis* from Velyka Komyshevakha (adapted from Alekseeva 1977).**Figure 4.** A, side view of the mandible VGr-1465 of *Pliotragus ardeus* from Valea Grăunceanului; B, side view of the mandible FSL-5008 of *Gallogoral meneghinii* from Senezè.

Table 2. Measurements of mandibles of *Pliotragus ardeus* from Valea Grăunceanului (VGr-1465) and *Gallogoral meneghini* from Sènèze (FSL-5008).

Measurements	VGr-1465 sin	VGr-1465 dx	FSL-5008
L P ₂ -M ₃		114.0	106.2
L M ₁ -M ₃ (at base)	71.8	71.4	
L M ₁ -M ₃ (at occlusion)	70.5	68.3	68.0
L mandibular body		280.0	
L diastema		71.5	60.0
L P ₂ _ for. mentale		39.0	
L M ₃ _ proc. angularis	82.0	82.0	
H diastema		22.0	
H under P ₂		37.5	32.3
H under M ₁	33.3	35.5	38.2
H under anterior edge of M ₃	46.4	ca. 42.0	40.7

**Figure 5.** Lower cheek teeth crown measurements of *Pliotragus ardeus* from Valea Grăunceanului compared to Caprinae from various Early Pleistocene sites: *P. ardeus* from Sènèze (adapted from Duvernois and Guerin 1989), *Procambtoceras brivatense* from Sènèze (adapted from Duvernois and Guerin 1989), *Soergelia brigittae* from Apollonia 1 (adapted from Kostopoulos 1997), *Soergelia minor* from Venta Micena (adapted from Crégut-Bonnoure and Dmitrijevic 2006), *Soergelia elisabethae* from Süssenborn (adapted from Kostopoulos 1997), *Soergelia intermedia* from Trlica (adapted from Crégut-Bonnoure and Dmitrijevic 2006) and *Soergelia sp.* from Dmanisi (adapted from Vekua 1995).**Figure 6.** *Pliotragus ardeus* from Valea Grăunceanului; occlusion view of upper cheek teeth series P₂-M₃ of the mandible VGr-1465: A, left tooth row; B, right tooth row.

Therefore, the shape of the third lobe of M_3 is not a secure diagnostic character of *Pliotragus*.

Postcranials

The complete radius VGr.0926 is rather long and relatively slender (Figure 7; Table 3). The scatter diagram shows that length and diaphysis robustness of the radius from VGr is close to that of *P. ardeus* from S n ze (Figure 8A). The general size of *P. ardeus* radii is relatively larger than in *Gallogoral*. Notably *Gallogoral* and, apparently, *Pliotragus* (though data for the later genus are insufficient) do not show strong sexual dimorphism in the proportions of the radius that characterise modern *Capricornis* and *Nemorhaedus* (Figure 8A).

Metapodials of *P. ardeus* are moderately elongated and characterised by broadened distal parts of the diaphysis and distal epiphysis. Metacarpals of *P. ardeus* from VGr (Figure 9-A1) are absolutely and relatively longer than in *G. meneghinii* from S n ze and characterised by a relatively slightly narrower upper diaphysis than in *G. meneghinii* (Table 4). The size difference between two complete metacarpals of *P. ardeus* from VGr is comparable to the expression of sexual dimorphism in the relatively large sample of *G. meneghinii*

from S n ze (Figure 8-B). Thus, it is likely that the larger metacarpal VGr.1612 belongs to a male, while the smaller metacarpal VGr.0383 is female.

Metatarsals of *P. ardeus* are comparatively long (Figure 10-A1), much longer than in *G. meneghinii* from S n ze and even slightly longer (but also more slender) than in *M. latifrons* (Table 5). The proximal epiphysis of the metatarsal from VGr is characterised by a specific medioanterior incision (Figure 10-A2) that we regard as an important morphological feature distinguishing *Pliotragus* from *Soergelia*. According to Kostopoulos (1997), the metatarsal of *Soergelia* from Apollonia-1 is characterised by a regularly rounded proximal epiphysis. Unlike *Soergelia*, the metapodials of *Pliotragus* from VGr are characterised by a narrower intertrochlear incision.

The left astragalus VGr.0938 of *Pliotragus ardeus* is characterised by a pronounced and strong medial condyle with a tibial shelf on the medial ridge of the proximal trochlea (Figure 11-A). This character is shared with *Rupicapra rupicapra* and *Ovis orientalis* (Gromova 1960, fig. 62) and possibly may be regarded as a supporting argument for inclusion of *P. ardeus* in Rupicaprini. This condyle with a tibial shelf is not present in *G. meneghinii* (Gu rin 1965, pl. LXIV). Unlike *R. rupicapra* and *G. meneghinii*,

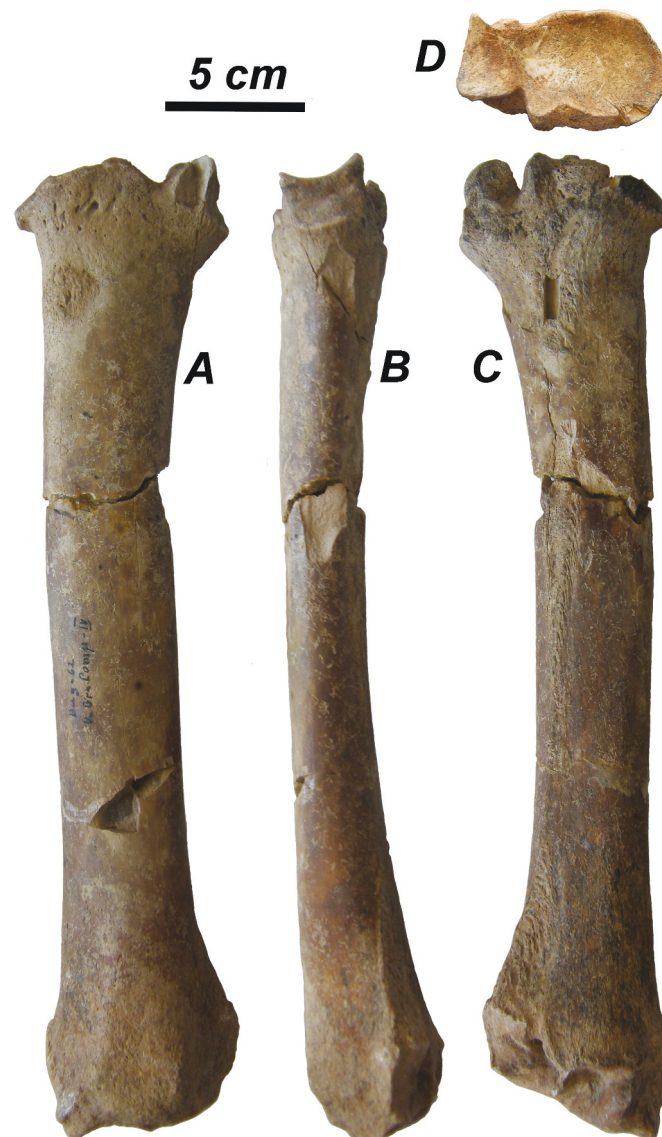
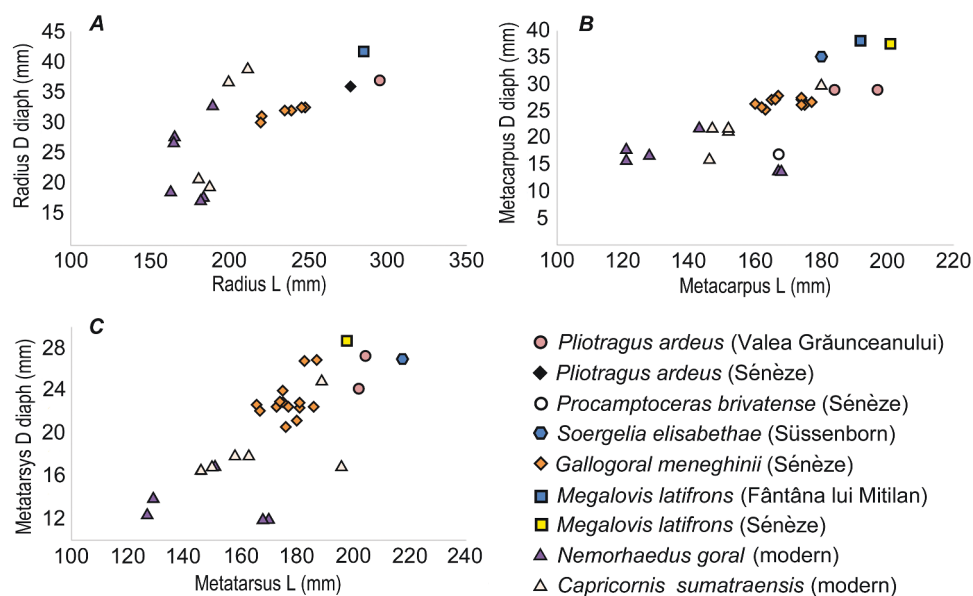


Figure 7. *Pliotragus ardeus* from Valea Gr unceanului; left radius VGr-0926: A, anterior view; B, medial view; C, posterior view; D, proximal view.

Table 3. Measurements of radii of the bovids from Valea Grăunceanului and Fântâna lui Mitilan.

Measurements	<i>Pliotragus ardeus</i>				<i>M. latifrons</i>	<i>O. moscatus</i>
	VGr-0930	VGr-0926	VGr-2284	VGr-2402	FM-0094	Dawkins (1872)
L maximum		295.0			290.0	299.7
L lateral		277.0			285.0	
DLM proximal	54.0	63.0			69.4	71.1
DAP proximal	26.6		30.0	28.7	36.6	20.3
DLM articulation	50.1	60.7				
DLM diaphysis	30.1	37.0	33.0		41.7	
DAP diaphysis	17.2	25.5	18.0			
DLM distal		57.0			63.5	
DAP distal		40.1			49.0	

**Figure 8.** Scatter diagram of long bone measurements of *Pliotragus ardeus* from Valea Grăunceanului and *Megalovis latifrons* from Fântâna lui Mitilan compared to fossil and modern Caprinae. The data on *Gallogoral meneghinii*, *Pliotragus ardeus*, *Procambtoceras brivatense* from Sénèze, modern *Nemorhaedus goral* and *Capricornis sumatraensis* are adapted from Guérin (1965). The data on *Megalovis pivetaui* from Shanshenmiaozui are adapted from Tong et al. (2022)

the astragalus of *P. ardeus* is characterised by strong development of a medial bulge at the collum tali. The maximum height of the astragalus at the lateral ridge of the proximal trochlea is 44.5 mm; the height of the astragalus at the trochlear groove is 37.5 mm; the height at the medial ridge of the trochlea is 43.5 mm; the distal breadth is 28.8 mm; the anteroposterior diameter of the distal trochlea on the medial side is 25.8 mm.

Tribe Ovibovini Gill, 1872

Genus *Megalovis* Schaub, 1923

Megalovis latifrons Schaub, 1923

Site

Fântâna lui Mitilan.

Horn core

The distal portion of the horn core FM.0090 is significantly compressed and has two well-expressed anterior and posterior keels (Figure 12). The horn-core tip is rather rounded in dorso-ventral

view. The preserved part of the horn core does not show any sign of bending or torsion. The cross-section of the horn-core fragment is lens-shaped. The anteroposterior measurement of the horn-core fragment at its proximal part is 43.0 mm, the horn-core thickness at the same level is 32 mm. The total length of the horn-core fragment is 77 mm.

The comparison of the horn core from FM with the type specimen of *M. latifrons* from Sénèze reveals significant morphological differences. The horn cores of the type specimen are thinner, less compressed and generally characterised by a cylinder-shaped proximal part and an oval cross-section of the distal portion (Schaub 1943). A weak rib is present only on the anterior side of the horn core. This difference may be explained by strong sexual dimorphism that is characteristic of Ovibovini. According to Crégut-Bonnoure and Dmitrijevic (2006), the holotype of *M. latifrons* belongs to a young female. The shape and size of the horn core from FM approaches that of the male specimen from Trlica described by Crégut-Bonnoure and Dmitrijevic (2006) as *M. balcanicus*. Therefore, we report the specimen from FM as a male horn core.

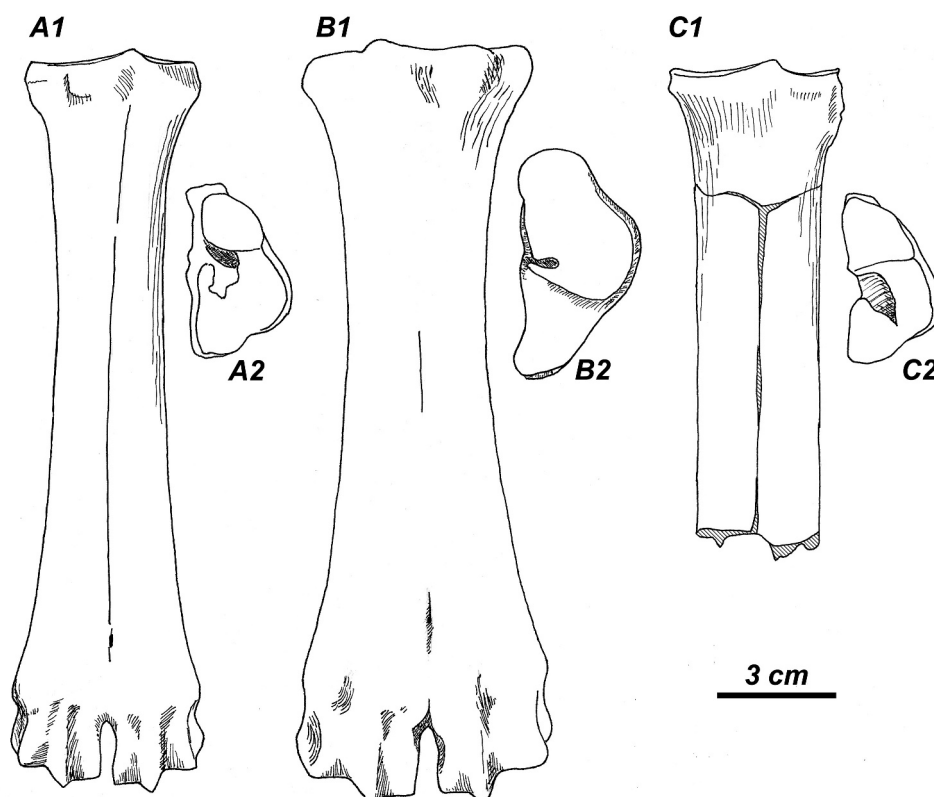


Figure 9. Metacarpal bones of bovids from Oltet River Valley: A, *Pliotragus ardeus*, VGr-0383; B, *Megalovis latifrons*, FM-0154; C, *Gazellospira torticornis*, VGr-1580; 1, dorsal view; 2, proximal articulation view.

Table 4. Measurements of metacarpals of the bovids from the Oltet River valley and Sénéze: *Pliotragus ardeus* from Valea Grăunceanului and *Megalovis latifrons* from Fântâna lui Mitilan compared to bovids from Sénéze.

Measurements	<i>Pliotragus ardeus</i>				<i>Megalovis latifrons</i>		<i>Gazellospira torticornis</i> Sénéze (Guerin 1965)	
	VGr-0383 ♀	VGr-1612 ♂	VGr-2285 ♀	VGr-1596	FM-0154 ♂	Sénéze	n – M – SD ♂	n – M – SD ♀
L maximum	184.0	197.0			192.0	201.0	5–174.8 – 1.30	5–164.6 – 2.07
DLM proximal	43.0	46.7	41.5		56.4	56.0	5–42.6 – 0.43	6–40.7 – 1.09
DAP proximal	29.5		29.7		34.7	36.5	5–27.6 – 0.63	6–25.7 – 1.06
DLM minimum of diaphysis	27.0	28.7	27.2	28.1	36.4	37.5		
DLM at middle of diaphysis	29.0	29.0			38.0		5–26.7 – 0.56	5–44.0 – 1.3
DAP at middle of diaphysis	19.6	21.1		19.3	22.0	24.5	5–18.5 – 0.54	6–18.4 – 0.58
DLM at distal condyles	46.1	49.0			60.5			
DLM distal	46.7	49.6			63.6	60.5	4–45.0 – 0.57	5–44.0 – 1.29
DAP distal	26.4	30.0			32.4	33.5	5–26.6 – 0.65	5–25.6 – 0.38

Dentition

The isolated upper right fourth premolar (P^4) FM.0142 is characterised by a weak parastyle and metastyle if compared to Bovinae of similar size (*Leptobos* and *Eobison*). The lingual wall is not grooved; the protocone and hypocone do not show any hints of separation. The inner enamel wall of the protocone-hypocone is simple and, unlike *Pliotragus* and *Leptobos*, does not show any trace of folding. The specimen under study is distinguished from *P. ardeus*, *L. etruscus* and *Bison* (*Eobison*) sp. from Apollonia-1 by its relatively narrower crown (Figure 13). The occlusal length and breadth of the tooth crown are 17.8 and 17.2 mm, respectively. The tooth from FM is somewhat larger than the sample from Sénéze ($n = 2$) and corresponds to the largest specimens from Trlica ($n = 4$).

Postcranials

The complete right radius FM.0094 corresponds to the smallest specimens of *Leptobos* from the Upper Valdarno and Olivola but is clearly distinguished from *Leptobos* by generally more elongated proportions and shows a greater affinity in its size and proportions with radii of modern *Ovibos moschatus*. The radius from FM is relatively slender (proximal epiphysis breadth/total length ratio is 24.3%) as in modern *O. moschatus* (23.2–23.7% according to the data from Dawkins 1852 and Gromova 1950). The radius under study is clearly distinct from the more robust radii of *Leptobos* from Upper Valdarno and Olivola (average value of breadth/length ratio is 28.8%, $n = 20$) and *B. (Eobison)* from Capena and Dmanisi (29.5–29.7%, $n = 3$). The Oltenian specimen is just slightly

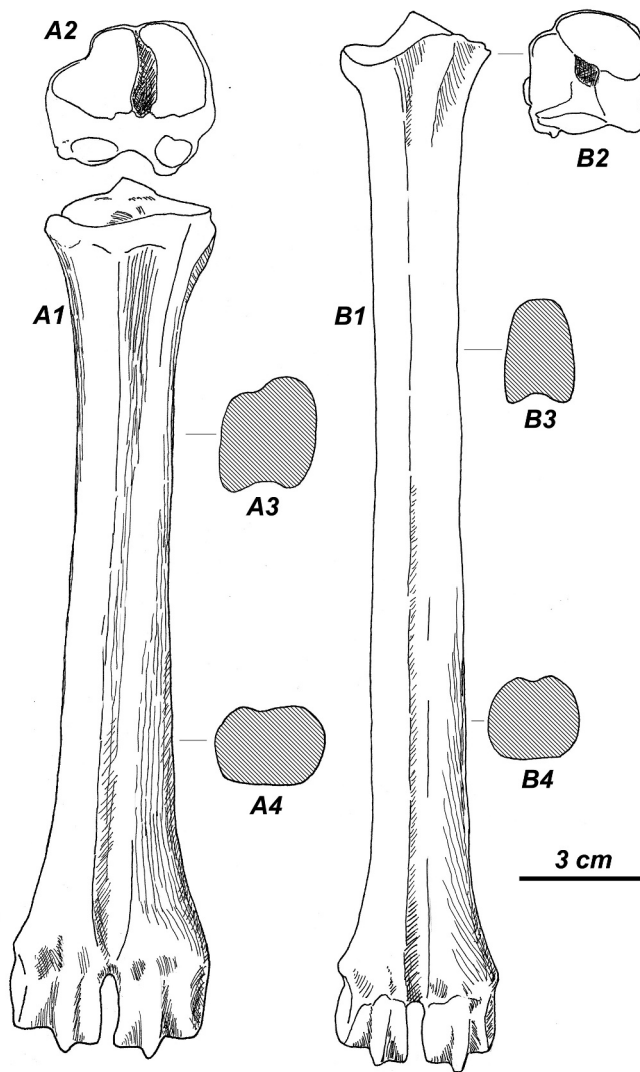


Figure 10. Metatarsal bones of bovids from Olteț River Valley: A, *Pliotragus ardeus*, VGr-0577; B, *Gazellospira torticornis*, VGr-0655; 1, dorsal view; 2, proximal articulation view; 3, cross-section shape of the proximal part of diaphysis; 4, cross-section shape of the distal part of diaphysis.

Table 5. Measurements of metatarsals of *Pliotragus ardeus* from Valea Grăunceanului compared to bovids from Sênèze and Olivola.

Measurements	<i>Pliotragus ardeus</i>				<i>M. latifrons</i>	<i>Gallogoral meneghinii</i>		
	VGr-0577	VGr-2397	VGr-0381	VGr-1756	Sênèze FSL-16894	Olivola ♂ (Schaub, 1928)	Sênèze n – M – SD ♂	Sênèze n – M – SD ♀
L maximum	202.0	204.5			198.0	185.0	6–182.0 – 3.79	7–172.3 – 4.07
DLM proximal	39.3	37.4	39.1	37.7	45.0		5–37.6 – 0.64	7–35.4 – 1.03
DAP proximal	37.4		38.0	35.6	42.0		5–32.6 – 1.31	7–30.7 – 1.39
DLM minimum of diaphysis	23.1	24.5	25.7					
DLM at middle of diaphysis	24.2	27.3			28.6		6–23.1 – 1.96	7–22.6 – 1.04
DLM at distal condyles	45.0	43.5						
DLM distal	46.0	44.4			51.0	46.0	7–43.4 – 2.00	7–24.2 – 0.58
DAP distal	27.1	22.8			32.0		7–25.6 – 1.50	7–20.5 – 0.35

longer than the complete radius of *Megalovis pivetaui* from Shanshenmiaozi (the Early Pleistocene of Nihewan, China) described by Tong et al. (2022).

The right metacarpal FM.0154 (Figure 9-B) is robust and significantly compressed in the dorsoplantar direction. The

upper third of its diaphysis is the narrowest part of the bone, then the diaphysis gradually broadens towards the distal end. The plantar surface of the diaphysis is somewhat concave below the upper epiphysis. According to Crégut-Bonnoure (2007), the metacarpal from FM is distinguished from the

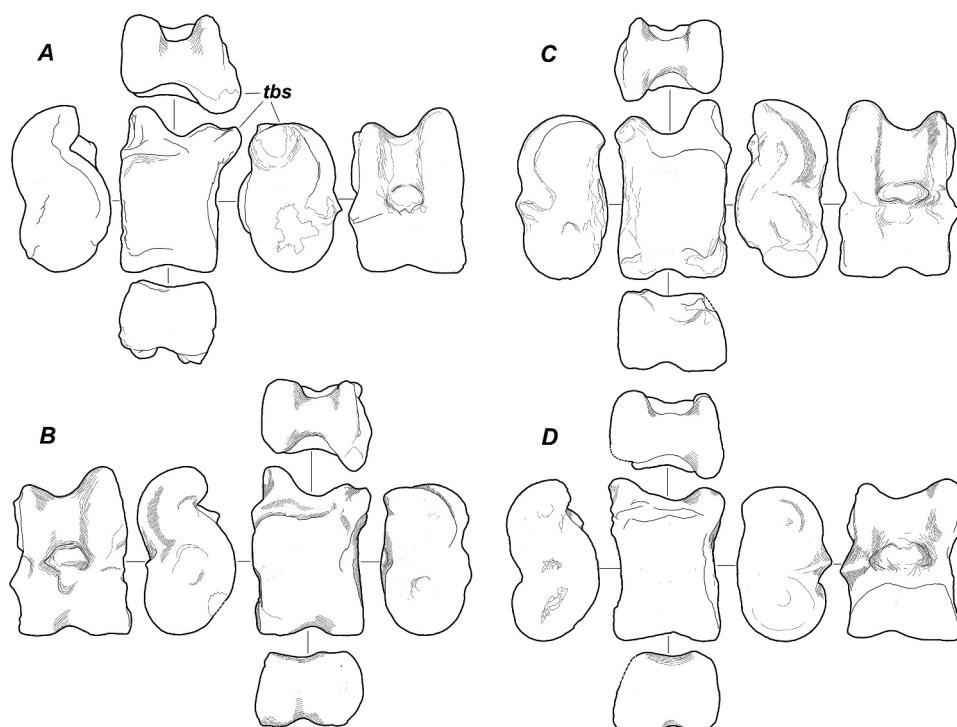


Figure 11. Astragali of ruminants from Valea Grăunceanului: A, *Pliotragus ardeus* (VGr-0938, left); B, *Alces* sp. (VGr-1151, left); C, *Rucervus radulescui* (VGr-1132, right); D, *Eucladoceros* sp. (VGr-1149, left); tbs, tibial shelf.

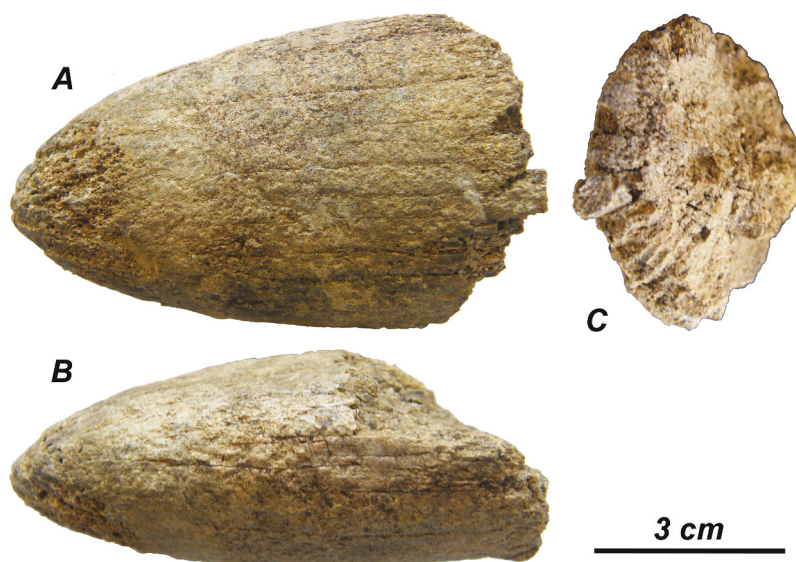


Figure 12. The distal portion of horn core FM-0090 of *Megalovis latifrons* from Fântâna lui Mitilan.

Sénèze material by a relatively narrower median articulation facet for the trapezoid-capitatum and a broader lateral articulation facet for the os hamatum. Apparently, this statement issued from a confusion, since the trapezoid-capitatum facet on the specimen FM.0154 is actually very broad and surrounds the synovial fossa (Figure 9-B2). The metacarpal from FM is somewhat shorter than the specimen from Sénèze described by Schaub (1943) and is characterised by the relatively broadest distal epiphysis (33.1%) among *Megalovis* specimens (30.1% in

M. latifrons from Sénèze; 28.1–29.9% [$n = 2$] in *M. pivetaui*; 30.8% in *M. wimani*). The complete metacarpal of *M. pivetaui* from Shanshenmiaozui described by Tong et al. (2022) is quite longer and more slender than the specimens from Romania and France. Metacarpals of *Praeovibos* are shorter and distinguished by their relatively broad epiphyses (the relative breadth of distal epiphysis ranges from 35.3% to 36.5% according to the data from Morris et al. 1993). The extreme robustness of the metacarpal FM.0154 is in accordance with the

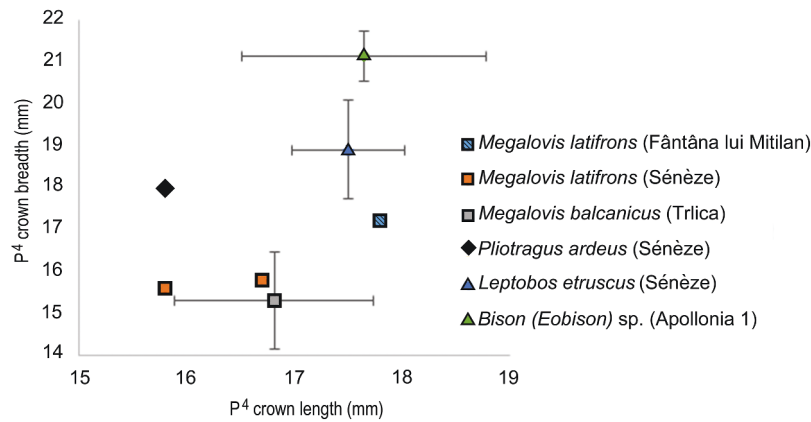


Figure 13. Measurements of the upper fourth premolar FM-0142 of *Megalovis latifrons* from Fântâna lui Mitilan compared to P⁴ samples of large Early Pleistocene bovids. Data on *Bison (Eobison) sp.* from Apollonia 1 are adapted from Kostopoulos (1997); the data on *Megalovis latifrons* from Sénèze and *Megalovis balcanicus* from Trlica are adapted from Crégut-Bonnoure and Dmitrijevic (2006); the data on *Leptobos etruscus* and *Pliotragus ardeus* from Sénèze are adapted from Duvernois and Guerin (1989).

assumption that the specimen belongs to a male. It is difficult to derive reliable conclusions on the systematic importance of the moderate differences in metacarpal proportions among *Megalovis* forms based on such a small sample of metacarpal bones that belong to sexually dimorphic bovids.

Subfamily Antilopinae Gray, 1821
Tribe Antilopini Gray, 1821
Genus *Gazellospira* Pilgrim & Schaub, 1939
***Gazellospira torticornis* (Aymard, 1854)**

Site

Valea Grăunceanului.

Postcranials

The distal epiphysis of the juvenile left radius VGr.0930 is shed, therefore, only estimated maximum length of the radius is reported here (Table 6). The radius is relatively long and thin. The ulnar incision on the proximal articulation surface is very shallow (Figure 14). The proximal articulation surface is narrowed anteroposteriorly.

The measurements of VGr.1589, a proximal metacarpus fragment (Table 6), are quite close to those of *P. ardeus*. However, the metacarpal bone of *Gazellospira* is distinguished from *P. ardeus* by

its much more slender diaphysis with parallel sided flanks that do not diverge distally as in *Pliotragus* (Figure 9).

Only one of three metatarsals (VGr.0655) is complete. The metatarsal is characterised by gracile and elongated proportions (Figure 10). The shape of proximal epiphysis is asymmetric due to the strong protrusion of its posteromedial part containing the articulation facet for the unciform. The lateral side of the proximal epiphysis is supplemented by a sharp condyle. The diaphysis looks very gracile due to the strong compression of its sides in its proximal third. The diaphysis cross-section shows a symmetric shape over much of its length. The plantar groove is rather shallow. The distal third of the diaphysis has a rounded cross-section with moderate anteroposterior compression. The diaphysis broadens sharply towards the distal epiphysis that forms strong condyles above the distal articulation blocks.

The remains of *Gazellospira* from VGr are somewhat larger than postcranial elements of *Pontoceros ambiguus* from Apollonia-1 and stand very close to the size of the postcranials of *Gazellospira torticornis* from Sénèze and Sesklo. *Gazellospira* from VGr is significantly larger than *Gazellospira sp.* from Çalta (Turkey), *G. torticornis* from Taurida Cave (Crimea) and *G. torticornis hispanica* from Fonelas-1 (Spain) (Figure 15). The similarity in limb size and proportions of *Gazellospira* from VGr with the sample from Sénèze permits us to ascribe the Romanian material to *G. torticornis*.

Table 6. Limb bones measurements of Athanassiou 2005) from Valea Grăunceanului.

Measurements	Radius VGr-0930 dx	Metacarpus VGr-1589	Metatarsus		
			VGr-0655 sin	VGr-1541 sin	VGr-0059 dx
L maximum	ca. 265		249.0		
DLM proximal	54.0	44.2	35.5	34.4	35.1
DLM articulation	50.1				
DAP proximal	26.6	30.1	35.0	36.2	
DLM of diaphysis		18.8	20.7		
DAP of diaphysis	17.2		25.0		
DLM at distal condyles			38.5		
DLM distal articulation			38.1		
DAP distal			25.0		

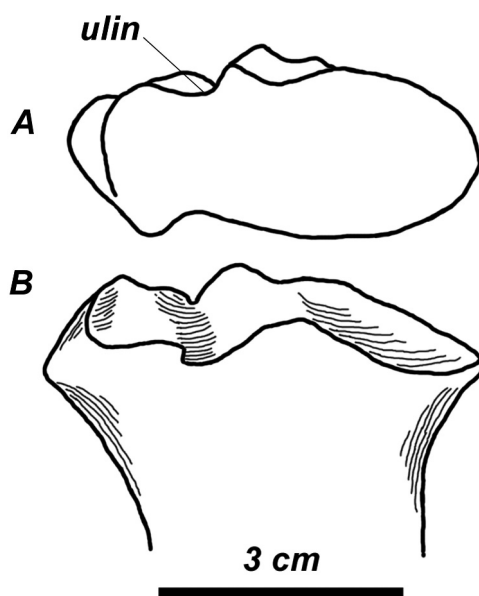


Figure 14. The proximal epiphysis of right radius VGr.0930 of *Gazellospira torticornis* from Valea Grăunceanului; *ulin*, ulnar incision.

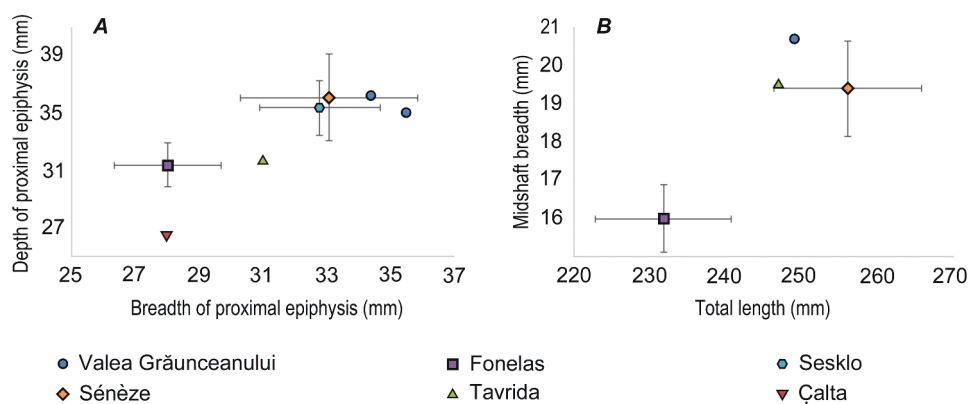


Figure 15. Scatter diagram of metatarsal measurements of *Gazellospira torticornis* from Valea Grăunceanului compared to the samples from Anatolia, Crimea, Greece and Western Europe; data on *G. torticornis* from Sénèze are adapted from Duvernois and Guerin (1989), data from Fonelas are adapted from Garrido 2008b), data from Sesklo, Calta and Tavrida are adapted from Athanassiou (2005), Bouvrain (1998) and Vislobokova et al. (2020), respectively.

Subfamily Bovinae Gray, 1821
Tribe Bovini Gray, 1821
Genus *Bison* Hamilton Smith, 1827
Subgenus *Eobison* Flerov, 1972

Bison (Eobison) sp.

Sites

Valea Grăunceanului, Olteț River Valley.

Horn core

The proximal horn core fragment VGr.1989 is compressed dorsoventrally, a character that represents an extreme condition for *Leptobos* but is quite common for primitive *Bison*. The specimen from VGr is more compressed dorsoventrally than horn cores of *Leptobos* from Upper Valdarno (Italy) and Leu (Romania). The ridges and furrows form a gentle but clear spiral torsion, which normally is not recorded in *Leptobos*. The size and shape of the horn core fragment from VGr is close to that of *Bison* from the Cromer Forest Bed Formation, England (NHML), but it is more compressed dorsoventrally. The shape and

measurements of the horn core in question are close to those of the type specimens of *B. (Eobison) tamanensis* and *B. (Eobison) georgicus*, as well as *B. (Eobison)* from Capena (Italy), Dolinskoe (Ukraine) and Semibalki (Russia) (Figure 16).

Postcranials

The measurements of the distal epiphysis of the metacarpal fragment Olt.0013 (distal breadth, 73.5 mm; distal depth, 42.0 mm) correspond to the measurements of *B. (Eobison) sp.* from Apollonia and the largest bovine specimens from Upper Valdarno that are distinct from the main sample of *Leptobos* (Figure 17b). The specimen under study also falls within the range of variation of *B. menneri* females; however, the relatively broad metacarpal diaphysis (44.7 mm) is broader than in both females and males of *B. menneri*. Therefore, the metacarpal fragment Olt.0013 likely belongs to a male individual of *Bison (Eobison) sp.*

Measurements of two damaged astragali, VGr.2292 (distal breadth, 56.0 mm; distal depth, 43.5 mm) and VGr.2123 (distal breadth, 51.1 mm; distal depth, 40.0 mm), are similar to those

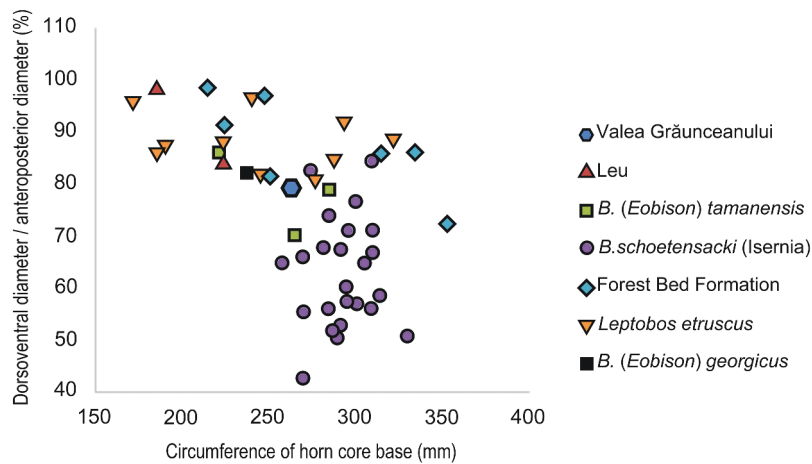


Figure 16. The degree of compression and circumference of the proximal fragment of horn core VGr.1989 of *Bison (Eobison)* sp. from Valea Grăunceanului compared to the samples of Early and Middle Pleistocene bovines from Europe. Data on *Bison* from Isernia are adapted from Sala (1986); data on *Bison (Eobison) georgicus* from Dmasini are adapted from Bukhsianidze (2005)

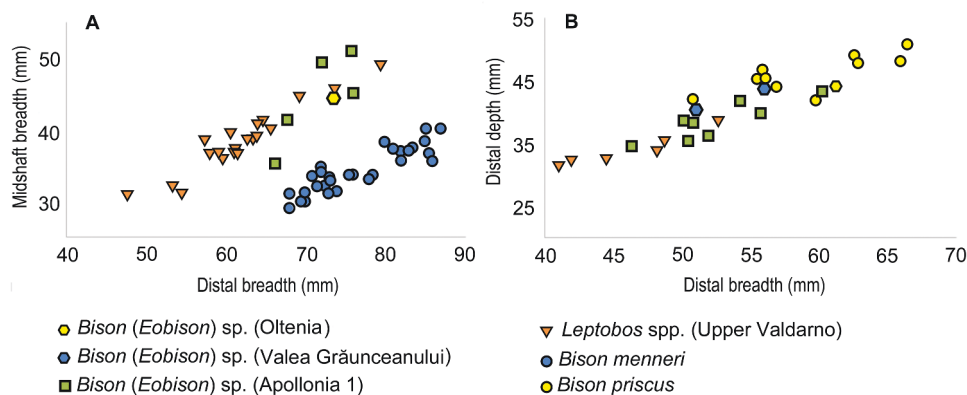


Figure 17. Scatter diagrams comparing the postcranial remains of *Bison (Eobison)* sp. from the Olteț River Valley: A, metacarpals; B, astragali. The data on *Bison menneri*, *B. priscus* and *B. (Eobison)* sp. from Apollonia 1 are adapted from Sher (1997) and Croitor (2010), respectively.

of the sample of *B. (Eobison)* sp. from the Early Pleistocene of Apollonia-I (Greece) and are substantially larger than the astragali of *L. etruscus* from Olivola (Figure 17-C). The well-preserved talus Nr. 2078 (Museum of Oltenia) from the Olteț River Valley (length, 89.0 mm; distal breadth, 61.0 mm; distal depth, 43.8 mm) corresponds to the largest specimens from Apollonia-I. The ratio distal breadth to total length in the specimen from Oltenia (68.5%) is relatively high and corresponds to the talus proportions of bisons from Apollonia-I ($M = 66.4\%$, $n = 8$) and Pirro Nord ($M = 66.7\%$, $n = 11$). Tali of *Leptobos* are somewhat narrower (Upper Valdarno: $M = 64.4\%$, $n = 7$; Olivola: $M = 63.5\%$, $n = 15$).

Family Cervidae Goldfuss, 1820
Subfamily Capreolinae Brookes, 1828
Genus *Alces* Gray, 1821

Alces sp.

Site

Valea Grăunceanului.

Antler

The single specimen ascribed to *Alces* is the quite unusual (aberrant?) almost complete shed antler VGr.2374 (Figure 18). The antler consists of a straight cylinder-shaped beam terminating in three cylinder-shaped undulating tines. Although the antler shape seems to be unusual, a close observation of its morphology allows us to understand its structural affinity and the antler's bauplan. The proximal part of the antler is just slightly compressed (diameters taken above the burr are 57.1×49.5 mm). The antler circumference above the burr is 158 mm. The beam cross-section becomes subtriangular shortly before the ramifications. The beam axis is perpendicular with respect to the burr plane. The first tine is situated at 128 mm from the burr. It is undulated, cylindrical in shape and is at least 140 mm (the tine tip is broken off). Apparently, this tine should be regarded as a homologue of the antler first ramification in Capreolinae deer. The distal bifurcation is situated at a short distance (33 mm) from the first tine. This slightly flattened portion of antler with a maximum diameter of 60 mm is a homologue of the second beam segment between the first ramification and the distal fork in other representatives of Capreolinae. The preserved tine of the distal fork is also cylinder shaped, with a regularly circular cross-section (tine diameters are 25.7 mm to 23.7 mm) and undulated. The length of the distal tine is 180 mm. The total length of the antler is 341 mm.

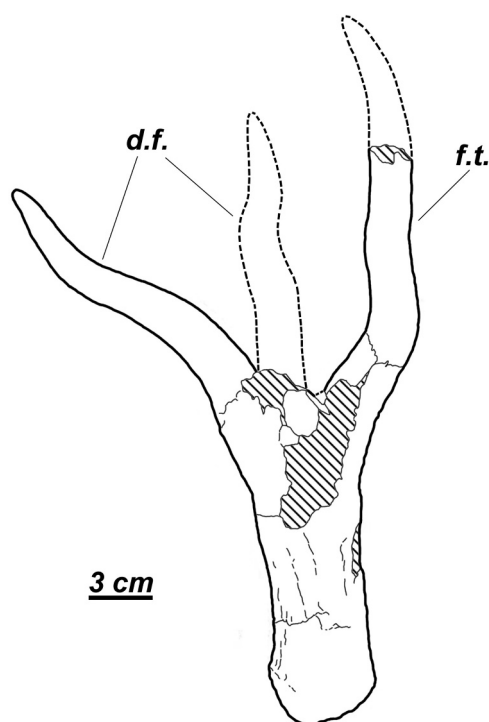


Figure 18. The shed antler VGr.2374 of *Alces* sp. from Valea Grăunceanului: f.t., first tine; d.f., distal fork.

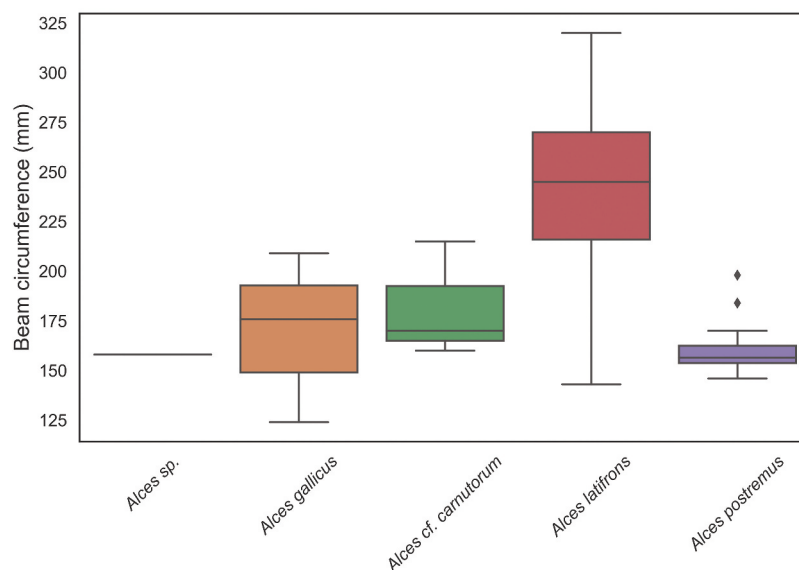


Figure 19. Antler circumferences of Pleistocene *Alces* compared; the data on *A. gallicus* are adapted from Vislobokova (1986) and Nikolskiy and Titov (2002); the data on *A. latifrons* and *A. postremus* are adapted from Boeskorov (2001)

The antler VGr.2374 generally shows the basic three-pointed *Capreolus*-like antler bauplan with the very high position of the first ramification characteristic of the subfamily Capreolinae. The extremely short second segment of antler with respect to the first segment (between the burr and the first ramification) clearly aligns the antler in question with early representatives of the genus *Alces*.

The diameters and circumference of the antler beam from VGr fall within the range of variation of the antlers of fully grown *Alces gallicus* (Figure 19) and the specimen is somewhat smaller than the moose antlers from the Early Pleistocene site of Salcia, Moldova, that is defined here as *A. cf. carnutorum*. The beam circumferences of the three specimens stored in the Institute of Zoology, Chişinău (Salcia II 2002, SAL-219, and

Table 7. Astragalus measurements of *Alces* sp. from Valea Grăunceanului and *Alces latifrons* from Mosbach (Stuttgart).

Measurements	Valea Grăunceanului		Mosbach			
	VGr-1151	VGr-1154	32,861/79	32,861/81	32,861/80	32,861/18
L max	57.6		100.2	98.5	100.9	93.3
DLM dist	37.5	37.5	60.5	62.0	61.4	58.0
DAP dist	28.8	28.8				

Salcia II 2002-b) are 160, 170 and 215 mm, respectively. The antler portion between the burr and the first ramification is remarkably short: the beam circumference to beam length ratio is 123.4%. This ratio varies in *A. gallicus* between 33.8% and 54.1% (Vislobokova 1986; Abbazzi et al. 1999; Boeskorov 2001; Nikolskiy and Titov 2002). In *A. latifrons*, this ratio varies between 64.6% and 100.0% (Johnston 1874; Kahlke 1969).

The relatively short beam and undeveloped distal palmation in the VGr.2374 antler are remarkable. This morphology may suggest that the specimen under study is not fully grown. Its beam diameters correspond to medium size antlers of *A. gallicus* and it is more robust than the smallest (juvenile) antler of *A. latifrons* (the antler from Tiraspol 1/61); therefore, one can assume that the antler from Valea Grăunceanului is not a juvenile. Therefore, the remarkably short antler beam and undeveloped antler palmation could be interpreted as derived from an older individual (senile) or that the antler developed on an individual living in poor ecological conditions. Similar morphological variants of antlers derived from older individuals are reported for modern *A. alces* (Sokolov 1959; Boeskorov 2001).

Postcranias

Two left astragali (VGr.1151 and VGr.1154) show specific diagnostic characters of *Alces*, such as the tibial shelf on the medial ridge of the proximal trochlea and the well-pronounced distal intracephalic fossa (Gromova 1960; Breda 2005) (Figure 11-B). The astragali of *A. latifrons* from Mosbach are characterised by the same specific diagnostic characters (the tibial shelf and intracephalic fossa) but are significantly larger (Table 7). The astragalus VGr.1151 is relatively shorter and broader when compared to the sample from Mosbach (Table 7): the distal breadth to maximum length ratio in the specimen from Valea Grăunceanului is 65.1%, while in *A. latifrons* from Mosbach this ratio varies between 60.4% and 62.9% ($M = 61.6\%$, $n = 4$). Unlike modern *A. alces*, the astragali of Early Pleistocene moose from VGr are more robust and lack a specific lateral notch visible from dorsal view (Gromova 1960: fig. 57-A).

Subfamily Cervinae Goldfuss, 1820

Genus *Eucladoceros* Falconer, 1868

Eucladoceros dicranios Nestii, 1841

Site

Valea Grăunceanului.

Antlers

The left shed antler VGr.2126 (Figure 20) lacks the distal portion above its first crown tine. The antler surface is somewhat weathered. Immediately above the burr, the antler beam is directed backwards and a little laterally. The basal tine is set quite close to the

burr and is characterised by a side compression that resulted in an oval cross-section of the tine. The characteristic *Eucladoceros* accessory prong in the area of basal ramification is situated on a well-expressed rib connecting the basal tine and the main beam and extending until the first crown tine. The antler beam between the basal ramification and the first crown ramification is moderately anteroposteriorly compressed; its cross-section is irregularly rounded here. The first crown tine is compressed from the sides and broadens distally, suggesting a further bifurcation of the distal portion of the tine. Measurements of the antler from VGr do not reveal any particular distinguishing features: the Romanian *E. dicranios* is very close in size to the type specimen from Upper Valdarno (Italy) and falls within the range of variation of the sample from Liventsovka (Table 8). The rather short distance between the burr and the first crown tine is the only character that distinguishes the antler from VGr from *E. dicranios* from Upper Valdarno and Liventsovka, but this feature seems to be quite variable in *E. dicranios*.

The heavily damaged proximal part of a right antler VGr.2026 is another specimen that shows a typical *E. dicranios* morphology: its accessory prong in the area of the basal ramification is situated medially from the antler beam axis.

Eucladoceros ctenoides falconeri (Dawkins, 1868)

Site

Valea Grăunceanului.

Antlers

The shed left antler VGr.2373 is broken just before the first crown tine ramification (Figure 21A). The beam deviates from the burr laterally and bends backward at the level of the first ramification. The antler base is rounded-triangular, with a somewhat flattened posterior side. The long and unbranched first tine is situated rather high above the burr. The first ramification height (Table 9) is almost twice the antler base diameter and falls within the range of variation of the sample from Sènèze (65.0–120.0 mm; Heintz 1970). The angle of the first ramification is 105°. The cross-section of the first tine is oval in its proximal portion and irregularly circular in its distal part. A small accessory prong is situated above the first ramification somewhat medially at a distance of 10 cm. This prong is cone-shaped and quite small, ca. 2 cm in length. The antler beam cross-section between the basal and accessory tines is irregularly oval. More distally, above the accessory prong, the beam becomes compressed from the sides. The medial side of the beam is more convex than the lateral one. The distance between the first ramification and the crown part is quite long, not less than 31 cm.

Most probably, the poorly preserved antler beam fragment VGr.2037 (Figure 21 B), which has a slightly bent cone-shaped tine, also should be ascribed to this form.

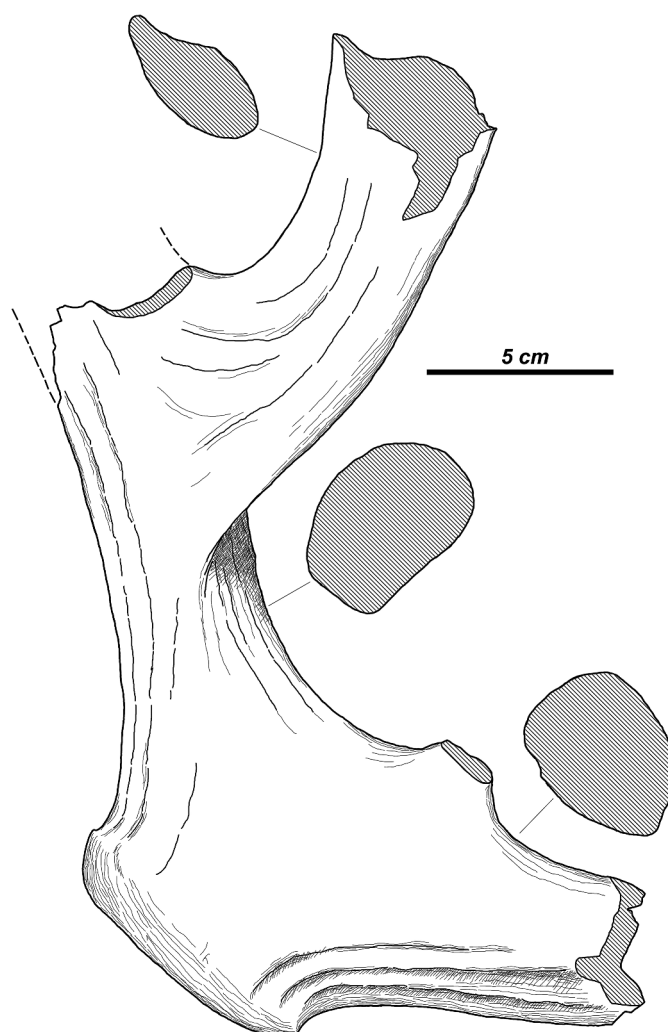


Figure 20. The left shed antler VGr-2126 of *Eucladoceros dicranios* from Valea Grăunceanului.

Table 8. Measurements of antler remains of *Eucladoceros dicranios*. Measurements of *E. dicranios segdwickii* from Bacton are adapted from Falconer (1868).

Measurements	VGr-2126	VGr-2026	IGF-270	LIV-531	LIV-1600	LIV-1218	Bacton
DAP above burr	75.0		71.0	55.4	72.0	50.7	
DLM above burr	53.6		67.5	62.3	59.5	40.5	
H basal ramification (lateral side)	81.7		80.0	60.0	93.0	101.3	171.5
H basal ramification (medial side)	84.0						
L burr – first crown tine	190.0		255.0	220.0			323.9
Circumference of beam between basal and crown tine	154.0						
D maximum of beam between basal and crown tine	48.3	48.1	63.4				
D minimum of beam between basal and crown tine	41.2	34.0	46.3				

Eucladoceros

The tine length should slightly exceed 10 cm, its basal diameter is 31.5 mm. The tine cross-section is regularly circular. This tine is interpreted here as a well-developed accessory prong (dorsal tine) similar to some specimens of *E. ctenoides falconeri* from Sènèze and Chilhac. The accessory prongs of the antlers CH3-1981-184 from Chilhac are characterised by similar size: the length and basal diameter on the right antler are 160 mm and 35.1 mm

correspondingly; the same measurements of the left antler are 156.0 mm and 30.4 by 28.4 mm.

The distal left antler fragment VGr.1834 (Figure 22) is a portion of the antler beam with the first crown ramification. The antler beam is compressed from the sides, while the ramification portion is strongly flattened; however, we do not exclude the possibility of crushing deformation of the specimen. The medial side of the beam is concave; the lateral side is more flattened. The flattened part of

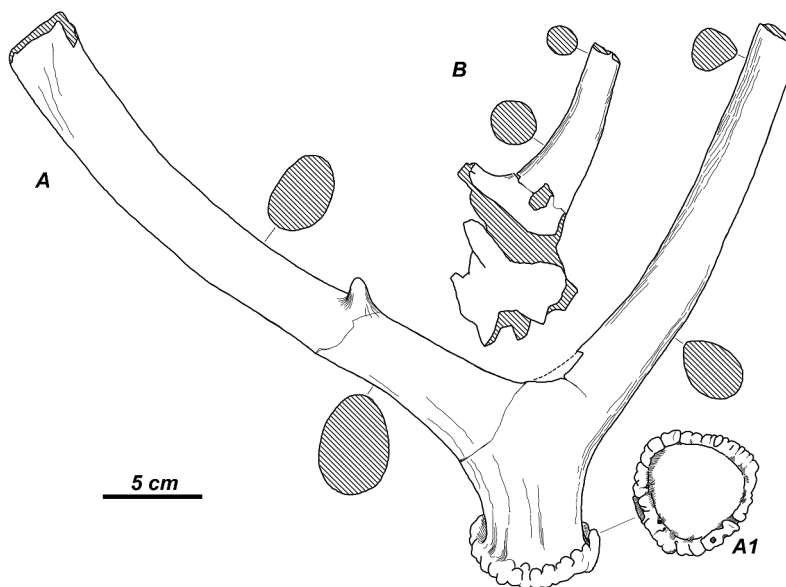


Figure 21. Antler fragments of *Eucladoceros ctenoides falconeri* from Valea Grăunceanului: A, the shed left antler VGr.2373; A1, basal view of the antler VGr.2373; B, the beam portion with accessory prong VGr.2037.

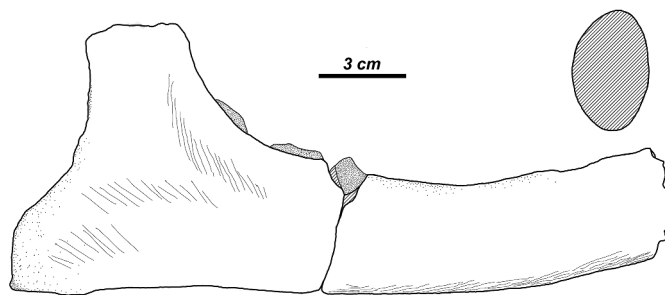


Figure 22. The distal fragment of left antler of *Eucladoceros ctenoides falconeri* from Valea Grăunceanului.

the antler with the crown ramification is slightly twisted medially. The angle of ramification is ca. 90°.

Based on their general morphology and measurements, the antler fragments from VGr are very similar to the samples from Norwich Crag (the type locality), Sènèze, Chilhac and Tegelen. The more or less straight (not S-shaped) basal tine is the only character that distinguishes the Romanian material from Western European samples. The antler remains from VGr are distinguished from *E. ctenoides ctenoides* by the comparatively high position of the first ramification, the long distance between the basal tine and the accessory prong and the long distance between the basal tine and the crown portion of the antler.

Eucladoceros sp.

Sites

Valea Grăunceanului, Fântâna lui Mitilan.

Postcranials

The proximal fragment of a right cervid metatarsal VGr.1757 is similar in size to *Rucervus radulescui*; however, it is clearly distinguished by some morphological details of the proximal epiphysis and

diaphysis. Unlike *R. radulescui*, the proximal articulation is characterised by a rounder and broader anterior side, while the diaphysis in its upper third has a more symmetric cross-sectional shape (Figure 23). The proximal epiphysis breadth is 40.4 mm, the epiphysis depth is 41.2 mm. The minimum diaphysis breadth is 23.6 mm.

Cranial material

The right frontal bone fragment VGr.2286 with pedicle is ascribed to *Eucladoceros* on the basis of the conspicuous robustness and shortness of the pedicle that falls within the range of variation of *E. ctenoides* from Sènèze according to the data provided by Heintz (1970). The pedicle cross-section is regularly circular; its antero-posterior and lateromedial diameters amount to 50.0 mm. The pedicle height is 25.7 mm (Figure 24).

Craniodental material

The right hemimandible FM.0091 (Figure 25) is characterised by a primitive unmolarized P₄ and a quite short premolar series (PP/MM – 58.8%). The premolars show a specific feature that is seen in *Eucladoceros* and distinguishes the specimen in question from *Rucervus* (*Arvernoceros*): the length of the premolars diminishes from P₂ to P₄, while in *R. (Arvernoceros) radulescui* P₂ is the shortest tooth

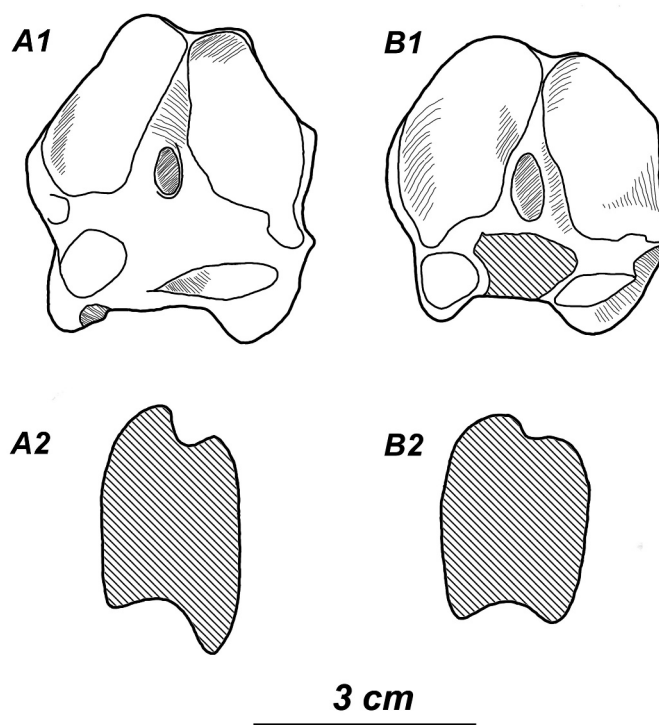


Figure 23. The proximal epiphysis (1) and the cross-section in upper third of diaphysis (2) of large deer from Valea Grăunceanului: A, *Rucervus (Arvernoceros) radulescui* (VGr-1553); B, *Eucladoceros* sp. (VGr-1757).

Table 9. Measurements of antler remains of *Eucladoceros ctenoides falconeri* (Dawkins, 1868) from Valea Grăunceanului compared with antlers from Chilhac (CH3, France), the Red Crag and Norwich Crag (BM, England).

Measurements	VGr.2373	VGr.1834	CH3-1981-184 (dx)	CH3-1981-184 (dx)	BM33509 (holotype)	BM15696
CFR above burr	155.0				108.0	125.0
CFR above first tine	136.0					
DAP burr	65.0		67.5	71.2		
DLM burr	61.0		67.5	70.4		
DAP above burr	51.1		56.3	57.0	33.7	42.7
DLM above burr	46.2		53.7	60.5	29.2	40.0
H lateral of first ramification	97.2		103.8	101.2	76.7	75.0
H medial of first ramification	88.0					
L basal ramification – accessory prong	100.0		220.0	260.0	78.3	81.0
DAP beam above accessory prong	43.4	38.0	50.2			
DLM beam above accessory prong	36.0	25.7	44.2			

and P₄ is the longest tooth of the premolar series. The dental measurements provided by Spaan (1992) demonstrate that the relatively short P₄ and long P₂ are characteristic of *Eucladoceros* from Western Europe. The isolated M₃ FM.0135 also should be assigned to this cervid form. The absence of antler remains does not allow species determination and its attribution to the genus *Eucladoceros* remains uncertain.

Genus *Rucervus* Hodgson, 1838

Subgenus *Arvernoceros* Heintz, 1970

Rucervus (Arvernoceros) radulescui Croitor, 2018

Sites

Valea Grăunceanului, La Pietriș, Slatina, Slatina-2.

Antlers

A proximal right antler fragment Sla.0002 with part of a pedicle comes from the fossiliferous site near Slatina. The antler beam is directed sideward immediately from the burr and its axis forms an angle of 78° with the burr plane. The antler becomes appreciably flattened in the area of the first ramification, which is situated very high above the burr: the first ramification height exceeds ca. three times the anteroposterior diameter of the antler above the burr. The antler beam turns backward from the first ramification and forms an angle of 120° with the first (basal) tine. The preserved part of the pedicle is slightly compressed anteroposteriorly.

The sample of antler remains from VGr provides additional information on the morphology and individual variation of the antlers. Generally, the robustness of the antlers and the height of

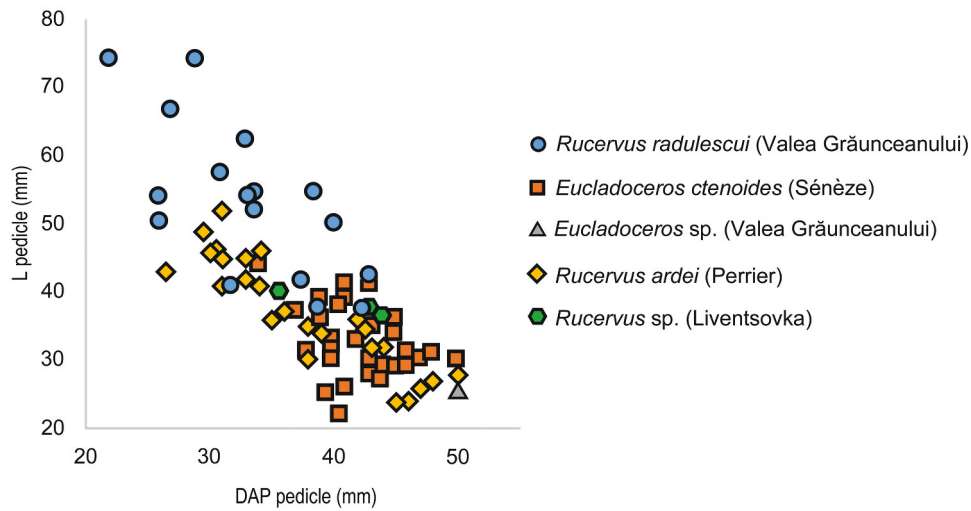


Figure 24. Anteroposterior diameter of pedicles of *Rucervus (Arvernoceros) radulescui* and *Eucladoceros* sp. from Valea Grăunceanului plotted against pedicle length. Data on *Rucervus (Arvernoceros) ardei* from Perrier and *Eucladoceros ctenoides* from Sênèze are adapted from Heintz (1970)

the first ramification of *R. radulescui* are very similar to those of (including the antler from Slatina) bears an atavistic additional



Figure 25. The right hemimandible FM.0091 of *Eucladoceros* sp. from Fântâna lui Mitilan.

Table 10. Antler measurements of *Rucervus (Arvernoceros) radulescui* from Valea Grăunceanului and other sites of the Dacian Basin.

Measurements	SLA-0002 dx	Slatina-2; nn	VGr-1926 sin	VGr-2050 sin	VGr-0936 sin	VGr-1880 dx	VGr-2133	VGr-2036 dx	VGr-1999 sin	VGr-2045 sin	OLT-0001 dx
DAP above burr	52.5	60.3	37.4	49.4	38.5	48.3	45.2	43.5	53.5		52.5
DLM above burr	52.0	46.0	33.0	46.5	35.0		42.0		47.2		51.2
H first ramification lateral	112.0	133.0		77.0	85.7			106.0			
H first ramification medial	130.0	115.0		80.5	87.5	116.5					
DAP beam above ramification	41.0			41.6	29.0					45.0	
DLM beam above ramification	36.1			43.0	27.8					38.4	
CFR above burr	150.0	169.0	115.0	156.0	112.0		136.0		154.0		155.0
CFR above first ramification	132.0			135.0	94.0					141.0	

R. ardei from Perrier-Etouaires (Table 10). Unlike *R. ardei*, *R. radulescui* completely lost the supplementary prong on the first tine. Only one shed antler (VGr.2036) out of 12 specimens

prong at the base of the first tine. The antler fragment VGr.2007 preserves an almost complete first tine that attains more than 270 mm in length (the tip is broken off). The first tine in the

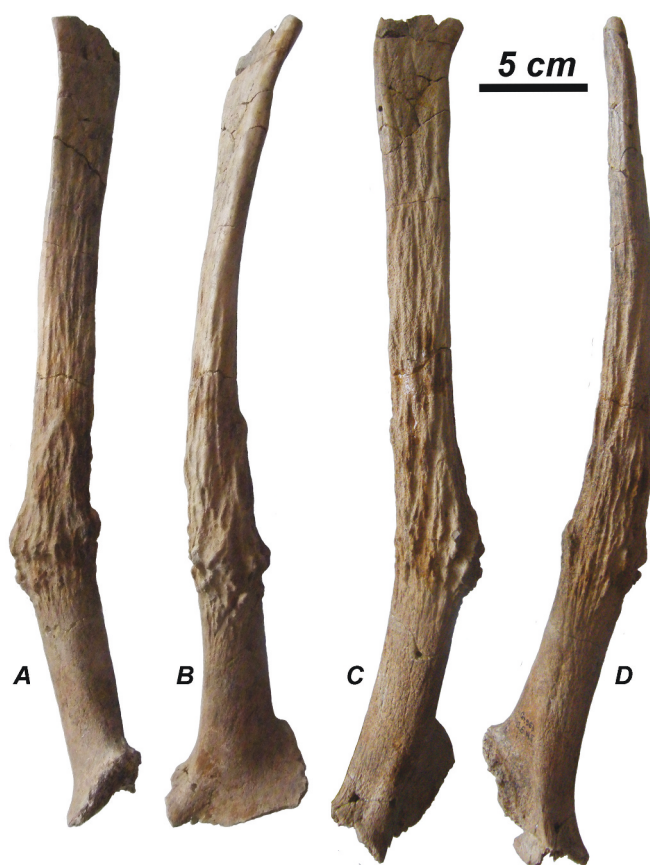


Figure 26. The juvenile antler VGr-2410 of *Rucervus (Arvernoceros) radulescui* from Valea Grăunceanului.

Romanian species is conspicuously long if compared to *R. ardei*. The length of the first tine in *R. ardei*, according to Heintz (1970), varies between 120 and 170 mm ($n = 4$). The shape of the first tine of the specimen VGr.2007 is rather cylindrical; it is moderately compressed from the sides at its basal portion and somewhat compressed anteroposteriorly in its distal part.

The left shed antler of a fully grown individual VGr.1948 is badly crushed and deformed; however it is interesting because it maintains most of its beam that is broken at the distal palmation base. The first ramification on the specimen VGr.1948 is situated at 146 mm from the burr, while the distance between the first ramification and the distal palmation is 350 mm. In the type specimen, which is an antler from a younger individual (Croitor 2018b): (Figure 1), this measurement attains only 290 mm.

Fragments of antler palmations are not common. We have at our disposal only a small palmation fragment VGr.2369 with a small cone-shaped prong; its thickness at the base is 15 mm; the length of prong is 150 mm.

The juvenile first-generation antler VGr.2410 is remarkable in its quite advanced shape for an antler from such an early stage of ontogenetic development (Figure 26). The antler is attached to a very long pedicle and characterised by a diffuse burr typical of first-generation antlers. The antler is broken at its distal end. The length of the preserved portion is 24 cm. The antler beam slightly deviates laterally and posteriorly from the pedicle axis. The first ramification is not present yet and at ca. 7 cm from the

base the antler becomes compressed from the sides and then extends into a flattened lobe. The posterior edge of the lobe is rounded, while the anterior end is quite sharp. The flattened part of the antler is twisted medially.

Cranium

The sample from VGr includes very young specimens with long pedicles, such as the frontal bone VGr.1881 attached to a first-generation antler, and large adult specimens with relatively robust pedicles (Table 11). The whole sample allows us to conclude that pedicles of *R. radulescui* are generally relatively long, significantly longer than in *E. ctenoides* from Sènèze with the samples overlapping very little on the scatter diagram (Figure 24). It is very interesting to note that the measurements of the pedicles of *R. radulescui* broadly overlap with those of *R. ardei* from the Pliocene of Perrier, but the material from Valea Grăunceanului contains a larger number of very long thin pedicles, suggesting a large proportion of young individuals in the sample from VGr. The most robust and shortest pedicles from VGr overlap with a small sample of *R. (Arvernoceros) sp.* from Liventsovka.

Males of *R. radulescui* are characterised by relatively narrow frontal bones as in *R. ardei*; their upper molar series length to frontal breadth ratios (based on mean values) are quite similar: 58.6% and 59.6%, respectively. However, *R. radulescui* skulls are conspicuously narrow at the frontal postorbital constriction compared to *E. ctenoides* from Sènèze and Chilhac and *E. dicranios* from



Figure 27. Mandible BUG-30108 of *Rucervus (Arvernoceros) radulescui* from Valea Grăunceanului: A, occlusion surface; B, side view.

Upper Valdarno and Liventsovka. The molar series length/frontal breadth indexes in these two *Eucladoceros* species amount to 54.8% and 52.2%, respectively. Modern European *C. elaphus* is characterised by relatively very broad frontals as in *E. dicranios*: its molar/frontal index is 52.7%. We do not exclude the possibility that the relatively narrow frontals in *R. radulescui* could be caused by the relatively high number of young individuals in the sample. Nonetheless, the mean value of this measurement from Valea Grăunceanului is very close to the frontal breadth of a rather old individual from Liventsovka (Table 11).

The anterior edge of the orbit in the female skull VGr.0894 is situated above the middle of M^3 as in *E. ctenoides* from Senez. A rounded lambdoid suture distinguishes *R. radulescui* from the pentagonal shape of this suture in *E. dicranios* (LIV-1218, Liventsovka). The facial portion of the cranium VGr.0812 of an aged individual is characterised by a moderately large fossa praeorbitalis (32.0 by 18.0 mm on the right side and 25.0 by 19.0 mm on the left side). The crushed skull of an older individual Nr. 2154 (old collection number 417) preserves a very large fissure nasolacrimalis (ca. 45 mm long) and a large fossa praeorbitalis of similar size. The nasal bones are very short: they extend caudally to the level of the posterior edge of M^1 and do not reach the level of the line connecting the anterior edges of the orbits. The poorly preserved palatal specimen with left maxillary and premaxillary bones VGr.0895 of an aged individual provides such important characters as the presence of the upper canine alveolus.

Mandible

The mandibular body below the tooth row is convex; the symphysis is elevated above the line connecting the posterior edge of the M_3 alveolus and the anterior edge of the P_2 alveolus (Figure 27). The general proportions of the mandibles from

VGr differ very little from *Eucladoceros* and *Cervus*. The sample from VGr does show a relatively higher mandibular body caudally: the mean ratio of mandible height measured below the anterior edge of M_3 to molar series length is 58.6% (range: 50.5–63.7%, $n = 4$). The same ratio is 54.3% (49.5–62.7%, $n = 6$) in *E. ctenoides* from Senez and 52.8% in the *Eucladoceros* sample from Upper Valdarno (44.6–68.0%, $n = 4$). *R. radulescui* is securely distinguished from *C. elaphus* by a relatively shorter diastema. In *R. radulescui*, the diastema length is roughly equal to the length of lower molar series, while in *C. elaphus* the diastema is always longer than the lower molar series.

Dentition

Upper molars are supplemented with a small enamel fold on the posterior wing of the metaconule sometimes mentioned in the literature as a ‘hypoconal spur’. An additional protoconal fold on the upper molars is not common and generally not visible at an advanced stage of wear. However, several small enamel folds are often present on the posterior wing of the protocone (Croitor 2018a): (Figure 5). Entostyles are moderate, cingula are never clearly developed. The angle between the lingual rib of the protocone and the mesostyle of the paracone on M^2 is 35°. This angle in *Eucladoceros* from Upper Valdarno (IGF-1145, IGF-1185) is ca. 40°, i.e. *Eucladoceros* maintains a more primitive condition of molar brachyodonty. The same angle in *C. elaphus* is 27–29° (measured on a sample of modern red deer from MNHN).

The lingual wall on P^2 is split and the protocone and metaconule are well-separated from one another. P^3 has a sharp lingual groove separating the protocone and metaconule, which are connected through an isthmus. The lingual groove on P^4 is weak; its metaconule is separated from the protocone

Table 11. Pedicle measurements and frontal breadth of *Rucervus (Arvernoceros) radulescui* from Valea Grăunceanului (VGr, BUG) and Slatina compared to *Rucervus (Arvernoceros)* sp. from Liventsovka (RGU). The total frontal breadths at constriction calculated from a single preserved frontal bone are marked with asterisk (*).

Measurements	SLA-0002 dx	Slatina-2; nn	VGr-1926 sin	VGr-2050 sin	VGr-0936 sin	VGr-1880 dx	VGr-2133 dx	VGr-2036 dx	VGr-1999 sin	VGr-2045 sin	OLT-0001 dx
DAP above burr	52.5	60.3	37.4	49.4	38.5	48.3	45.2	43.5	53.5		52.5
DLM above burr	52.0	46.0	33.0	46.5	35.0		42.0		47.2		51.2
H first ramification lateral	112.0	133.0		77.0	85.7			106.0			
H first ramification medial	130.0	115.0		80.5	87.5	116.5					
DAP beam above ramification	41.0			41.6	29.0					45.0	
DLM beam above ramification	36.1			43.0	27.8					38.4	
CFR above burr	150.0	169.0	115.0	156.0	112.0		136.0		154.0		155.0
CFR above first ramification	132.0			135.0	94.0					141.0	

by an isthmus and is supplemented by an inner enamel fold. *R. radulescui* is distinguished from *E. ctenoides* from S n ze by the absence of the inner enamel folds on the metaconule on P² and P³ and by the stronger separation of the protocone from the metaconule on P³ and P⁴: also, the lingual groove of P³ is deeper, and the isthmuses between the protocone and metaconule on both P³ and P⁴ are more strongly expressed. DP³ (VGr.2258) and DP⁴ (VGr.2262) are supplemented with a ‘hypoconal spur’ and well-developed entostyles.

The lower cheek tooth row in *R. radulescui* maintains a comparatively long premolar series with an unmolarized P₄. The mean value of the premolar/molar series ratio in the sample from Valea Gr unceanului is 68.6% (range of variation is 64.8–72.5%, n = 8). The relatively long lower premolar series of *R. radulescui* is similar to that of the mixed sample of *R. ardei* and *Praeclaphus perrieri* from Perrier (PP/MM = 68.1%, range of variation: 64.3–70.8%, n = 10). The same ratio is 63.6% (59.4–71.5%, n = 18) in *E. ctenoides* from S n ze and 61.3% (57.3–63.5%, n = 7) in *Eucladoceros* from the Upper Valdarno. The fourth lower premolar is unmolarized in all specimens of *R. radulescui* from VGr (n = 14) and, unlike *Eucladoceros*, the metaconid never fuses with the paraconid even in deeply worn teeth (Figure 27). The caudal extension of metaconid and its close contact with the entoconid in P₄ is a specific morphological feature of *R. radulescui* visible at all stages of dental wear.

Entostylids in lower molars may be moderately developed, but in most cases are vestigial.

Postcranials

The measurements and proportions of the long limb bones of *R. radulescui* (Table 12) are quite close to those of *E. ctenoides* from S n ze (Croitor 2018b). However, there are some differences in morphological details that require a careful study in the future. The shape of the metatarsal diaphysis cross-section distinguishes *R. radulescui* from *E. ctenoides*: in *R. radulescui*, the diaphysis cross-section is characterised by a more pronounced asymmetry than in *E. ctenoides* from S n ze (Figure 23). Unlike *Eucladoceros*, the astragalus of *R. radulescui* is characterised by a deeper and narrower intratrochlear notch with rounded outlines, weak development of the medial bulge at the collum tali and a sharper profile of the lower (distal) articulation trochlea (Figure 11).

Genus *Metacervoceros* Dietrich, 1938

Metacervoceros rhenanus (Dubois, 1904)

Metacervoceros rhenanus ssp. nov.

Sites

Valea Gr unceanului, Milcovu din Vale, Olte  River Valley.

Table 12. Statistical description of limb bones of *Rucervus radulescui* from Valea Gr unceanului.

Bone	Number	L	DLM prox	DAP prox	DLM diaf	DLM dist	DAP dist
Radius	n	13	45	45	15	11	5
	min	278.4	54.0	24.0	33.3	53.2	35.6
	max	310.8	67.3	37.0	42.5	60.1	42.7
	mean	299.8	62.6	33.2	37.8	56.6	39.9
	st.dev.	9.8	3.2	2.4	2.9	2.5	2.7
Metacarpus	n	29	69	66	28	46	45
	min	270.0	39.3	28.8	24.0	39.2	25.4
	max	318.0	52.7	39.4	34.5	52.0	36.6
	mean	287.9	45.9	33.7	28.4	47.5	30.9
	st.dev.	11.4	3.0	2.4	2.4	3.3	1.8
Astragalus	n	38				38	35
	min	49.7				25.1	24.0
	max	67.7				41.6	35.5
	mean	60.4				36.5	29.5
	st.dev.	4.2				3.1	2.5
Calcaneus	n	32				34	32
	min	121.6				23.3	33.0
	max	144.2				32.4	42.1
	mean	130.3				28.4	38.2
	st.dev.	6.1				2.0	2.3
Tibia	n	1				21	21
	min					50,0	39,0
	max					60,5	48,7
	mean	368.0				54,1	44,3
	st.dev.					7,4	5,4
Metatarsus	n	23	76	74HT	18	34	36
	min	287.0	36.7	39.3	20.3	45.1	30.0
	max	318.0	49.0	52.4	30.2	55.1	35.0
	mean	305.5	42.4	45.0	25.8	49.1	31.8
	st.dev.	8.4	2.6	2.4	2.2	2.2	1.2

Antlers

The shed antler fragments are characterised by a rather high position of the first tine and an acute angle of the first ramification that attains ca. 70° in the specimens VGr.1932 and Olt.0040. The antler surface is not pearled. The antlers from the Olteţ River Valley show a morphological affinity with *M. rhenanus* from Western Europe but are larger and characterised by a narrower angle of ramification. This angle in the sample from S n ze is quite acute too and varies between 50° and 90° (Heintz 1970). The angle of the first ramification in *M. rhenanus* from the type locality (Tegelen) is generally characterised by a broad range of variation (40°–105°; Spaan 1992). The narrowest angles of the first ramification in samples from Western Europe are recorded in juvenile antlers (Heintz 1970; Spaan 1992); however, the specimens VGr.1932 and Olt.0040 are adults. Unlike the type specimen of *M. rhenanus*, the antler beam in the sample from Romania is not curved backwards at the level of the first ramification and is slightly compressed anteroposteriorly above the first ramification. The Romanian sample is morphologically and biometrically close to the ‘*Rusa*-like’ deer described by Alekperova (1964) from the Early Pleistocene of Palantokan, Azerbaijan (Table 13). The angle of the first tine ramification in the antler from Palantokan is acute (75°), the antler beam is straight in its proximal part as in the antlers from Romania. The antlers from Romania and Azerbaijan fall within the size range variation of *M. shansius* from Shanxi (China) and share with the Chinese

species a high position of the first ramification. At the same time, the antlers under discussion are distinguished from *M. punjabiensis* from the Upper Siwaliks by the higher position of the first ramification.

Cranium

The neurocranium VGr.0900 belongs to a young male with unobliterated sutures and shed antlers. Pedicles are sloped backward and rather divergent. The pedicles may be described as moderately long: their lengths just slightly exceed their medio-lateral diameter. The relative pedicle length falls within the range of variation of *M. shansius*; however, only the oldest specimen from Shansi has shorter pedicles than in *Metacervocerus* from Romania (Table 14). Taking into consideration the younger individual age, one can assume that *Metacervocerus* from Valea Gr unceanului is characterised by shorter pedicles than *M. shansius*. The basioccipital is bell-shaped and broad at the pharyngeal tuberosities. The specimen is deformed, therefore only some cranial measurements are available (Table 15). The measurements and braincase proportions of the specimen VGr.0900 are very close to those of *Metacervocerus* from Milcovu din Vale (MV-161, University of Bucharest) and *M. shansius* from Shanxi (China). The braincase breadth to length ratio in the specimens VGr.0900 and MV-161 may be described as moderately short. The relative braincase

Table 13. Measurements of antlers of *Metacervocerus* from the Olte  River Valley compared to ‘*Rusa*-like’ cervid from Palantokan (Azerbaijan) and *Axis flerovi* from Navrukho (Tajikistan). The measurements of antlers from Palantokan and Navrukho are adapted from Alekperova (1964) and Vislobokova (1988), respectively.

Measurements	VGr-2009	VGr-1932	MV-161	OLT-0041	OLT-0040	Palantokan, nn	Navrukho, 3120–51	Navrukho, 3848/598-16
DAP above burr	45.0	37.8	34.6	42.5	36.0	40.5	54.0	48.0
DLM above burr	40.0	33.5	28.0	44.8	32.0	38.5	40.0	39.0
CFR above burr	141.0	118.0	107.0	137.0	113.0	135.0	150.0	138.0
H first ramification	74.0	69.3		113.8	84.5	79.2	58.0	41.5
DAP beam above ramification	36.0	27.2		32.0	23.8	37.5		
DLM beam above ramification	39.0	29.6		33.2	23.7	33.5		
CFR beam above ramification	119.0	107.0		112.0	80	120.0		

Table 14. Measurements of pedicles of *Metacervocerus rhenanus* ssp. from Valea Gr unceanului (VGr) compared to *Metacervocerus shansius* from Shansi (China).

Measurements	<i>Metacervocerus rhenanus</i> ssp.		<i>Metacervocerus shansius</i>			
	VGr-0900		22.726	14.333	10.518	10.520
	left	right				
DLM pedicle	31.0	31.0	43.0	32.0	40.0	26.0
DAP pedicle	30.1	27.2				
H pedicle	33.6	35.7	41.0	47.0	50.0	40.0

Table 15. Cranial measurements of *Metacervocerus rhenanus* ssp. from Valea Gr unceanului (VGr) and Milcovu din Vale (MV) compared to *Metacervocerus shansius* from Shansi (China). The data on *M. shansius* are adapted from Teilhard de Chardin and Trassaert (1937).

Measurements (mm) and braincase length ratio (%)	<i>M. rhenanus</i> ssp.		<i>Metacervocerus shansius</i>			
	VGr-0900	MV-161	22.726	14.333	110.518	10.296
Breadth at frontal constriction	102.7					
Braincase breadth behind pedicles	83.5	86.3	84.0	82.0	86.0	87.0
Distance bregma – inion	81.0	84.0	81.0	89.0	88.0	84.0
Breadth behind pedicles/bregma – inion (%)	103.1	102.7	103.7	92.1	97.7	103.6



Figure 28. The mandible VGr.2436/2440 of *Metacervocerus rhenanus* ssp. from Valea Grăunceanului: A, occlusion surface; B, side view.

Table 16. Measurements of the mandibles of *Metacervocerus rhenanus* ssp. (VGr.2436+ VGr.2440, right) and *Dama eurygonos* Azzaroli, 1957 (VGr-2435, right) from Valea Grăunceanului compared to *Axis flerovi* from Navrukho (Tajikistan) and *Dama eurygonos* from the Upper Valdarno (IGF). The data on *Axis flerovi* are adapted from Vislobokova (1988).

Measurements	<i>M. rhenanus</i> ssp.		<i>Dama eurygonos</i>				
	VGr.2436 + VGr.2440	<i>Axis flerovi</i> 3120/296; 3848–277/69	VGr-2435	IGF236	IGF8921	IGF8922	IGF8923
L P ₂ -M ₃	102.0	116.0	87.0	92.0	87.8	94.3	81.5
L P ₂ -P ₄	39.8	46.5	33.1	35.0	33.5	41.3	30.0
L M ₁ -M ₃	57.5	76.0	53.0	57.0	54.4	60.4	51.0
H under P ₂	21.8		18.7		26.2	22.1	24.6
D under P ₂	10.8		8.6				
H under M ₁			23.5		27.5	24.3	26.5
D under M ₁	13.7		13.0				
D under M ₂ /M ₃	15.2		14.5				
P ₂ L	11.2	13.0					
P ₂ D	7.0	7.5					
P ₃ L	15.0	16.7	11.2				
P ₃ D	8.2	10.8	7.0				
P ₄ L	13.6	16.8	12.2				
P ₄ D	9.8		8.6				
M ₁ L	16.0		15.3				
M ₁ D	11.0		9.0				
M ₂ L	18.7		18.0				
M ₂ D	11.8		10.3				
M ₃ L	23.1		21.8				
M ₃ D	11.5		10.8				
PP/MM (%)	69.2	61.2	62.5	61.4	61.6	68.4	58.8

lengths of *Metacervocerus* from VGr and Milcovu din Vale fall within the range of variation of *M. shansius* (Table 15) and *M. rhenanus* from Sènèze and Ceysaguet (87.9–110.8%; M = 101.7%; n = 4).

Mandible

The right ramus of mandible fragment VGr.2436/2440 preserves P₂-M₂ and an isolated right M₃ VGr.2440 that belongs to the same individual (Figure 28; Table 16). The mandible is characterised by a moderately long premolar series (the premolar to molar series ratio is 69.2%), which is very close to the ratio in the mandible of '*Cervus (Rusa) philisi*' from

Liventsovka (69.4%; Titov 2008) and *M. shansius* (69.2%; Teilhard de Chardin and Piveteau 1930). This ratio on the mandible from VGr is the same as the extreme maximum value in the sample of *M. rhenanus* from Sènèze (57.1–69.2%; M = 64.1%; n = 16) and is close to the mean value of the sample from Tegelen (66.6–73.1%; M = 69.6%; n = 6). Tooth row length places the mandible from VGr within the range of size variation of the small sample (n = 3) from Liventsovka and would place it among the largest specimens of *M. rhenanus* from Western Europe. The mandibular body below P₂ is relatively low (the mandible height to tooth length ratio is 21.4%) and falls within the range of variation of

the sample from S n ze (20.5–28.4%; M = 24.0%; n = 12), being similar to the proportions of the largest S n ze specimens.

Dentition

The fourth lower premolar (P₄) of the mandible VGr.2436 is characterised by a primitively low degree of molarisation: the metaconid is extended mesiodistally but is not fused with the paraconid, therefore the trigonid valley remains open. The metaconid of P₃ is well-expressed but does not extend mesiodistally as in P₄. The lower molars are supplemented with an anterior enamel ‘fold of compression’. The ectostylid on M₁ is well-developed, but it is quite vestigial on M₂. The M₃ has a well-developed anterior ectostylid and a vestigial posterior one.

Only two isolated upper cheek teeth from VGr belong to *Metacervocerus*. The left P² VGr.2444 is in the initial stage of wear (L, 13.3 mm; D, 13.0 mm) and is characterised by a deep vertical groove on the lingual wall, which separates the protocone from the hypocone, and the development of an inner enamel fold on the hypocone. The tooth crown is as broad as in *M. shansius*, but is much shorter, approaching in this respect the sample of *M. rhenanus* from S n ze described by Heintz (1970).

The right P⁴ VGr.2442 is characterised by a well-developed inner protoconal fold. The lingual wall is not grooved. The tooth is much smaller than P⁴ of *M. punjabiensis* and just slightly smaller than P⁴ of *M. shansius*. VGr.2442 (L, 12.2 mm; D, 15.6 mm) would be among the largest P⁴s of *M. rhenanus* from S n ze but still falls within the range of the standard deviation of the French sample.

Postcranials

Remains of postcranial bones are exiguous and include three metacarpal fragments from VGr: a distal fragment VGr.0057 (DLM dist, 39.3 mm; DAP dist, 29.2 mm), another distal fragment BUG-nn (DLM dist, 39.2 mm; DAP dist, 25.4 mm) and a proximal fragment BUG-9719 (DLM prox, 39.3 mm; DAP prox, 28.8 mm). The measurements of metacarpal bones correspond to the maximum values of the sample of *M. rhenanus* from S n ze.

Genus *Dama* Frisch, 1775

Dama eurygonos Azzaroli, 1947

Site

Valea Gr unceanului.

Antler

The proximal right shed antler fragment VGr.0933 is characterised by a rather low position of the first tine and an open angle of the first ramification (85 ). The beam cross-section is regularly circular. The antler surface is devoid of pearling, which is characteristic of another Early Pleistocene cervid of similar size, *Cervus nestii*. The measurements, the angle and the height of the first ramification of the antler VGr.0933 are similar to those of the holotype of *Dama eurygonos* from the Upper Valdarno and the fallow deer from Slobozia Mare, Lower Prut River Valley (the Republic of Moldova) (Table 17).

Mandible

The mandible VGr.2435 (Figure 29 A,B) fits the shape, size and proportions of *D. eurygonos* mandibles from the Upper Valdarno. The specimen from Valea Gr unceanului is characterised by a relatively long premolar series (the premolar/molar length ratio is 62.5%), which exceeds the premolar/molar ratio range in modern *Dama dama* (46.0–61.7%; M = 58.0%; n = 12) and falls within the range of variation of *D. eurygonos* from the Upper Valdarno (58.8–67.4%; M = 62.7%; n = 13) and *Croizetoceros ramosus* from Perrier-Etouvaires (56.9–70.2%; M = 64.7%; n = 11). The height of the mandibular body below M₁ relative to molar series length (44.3%) falls within the range of variation of *D. dama* (40.2–48.7%; M = 43.8; n = 12) and *D. eurygonos* from the Upper Valdarno (40.2–51.9%; M = 47.6%; n = 3).

Dentition

The fourth lower premolar (P₄) is molarized: the metaconid is completely fused with the paraconid, thus the anterior (trigonid) valley is closed. The parastylid and paraconid are not separated. P₃ is characterised by a strong metaconid that is extended mesially. The paraconid and parastylid of P₃ are clearly distinguished. Molars are supplemented with well-developed ectostylids and an anterior enamel ‘fold of compression’.

The isolated upper right third molar (M³) VGr.2441 is characterised by the presence of an entostyle and a small enamel fold on the metaconule (‘the spur of hypocone’ *vide* Heintz 1970). The angle between the lingual rib of the protocone and the rib of the paracone is 35 . The anteroposterior length of the tooth at the crown base is 13.3 mm, other measurements are indicated in Table 18. The dental measurements, morphology and the paracone-protocone angle of specimen VGr.2441 approach those of *Dama eurygonos* from Upper Valdarno.

Table 17. Measurements of antlers of *Dama eurygonos* from Valea Gr unceanului, Upper Valdarno (IGF, holotype) and Slobozia Mare (SM, IZC).

Measurements	VGr-0933	IGF-245	SM-26/20
DAP above burr	48.1	53.7	43.2
DLM above burr	41.0	42.2	40.7
H first ramification (lateral)	47.0	52.5	52.4
DAP beam above first ramification	28.6	34.4	
DLM beam above first ramification	27.7	31.5	
CFR above burr	145.0	170.0	132.0
CFR above first ramification	100.0	115.0	

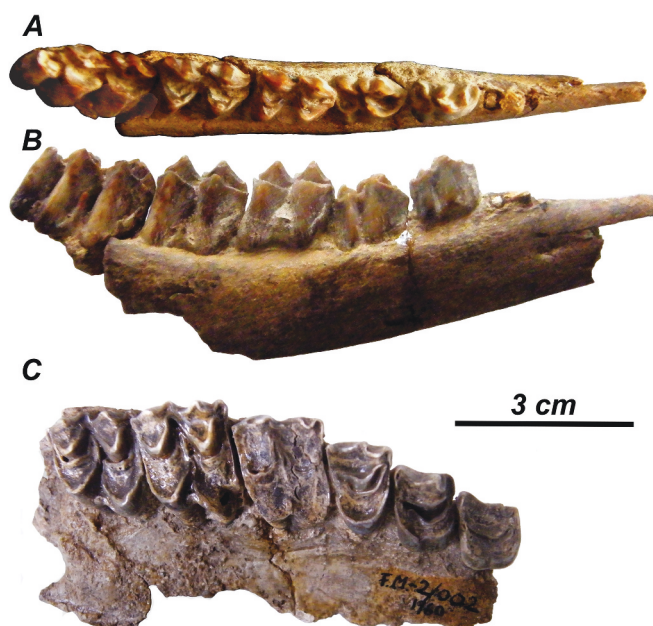


Figure 29. Fallow deer remains from the Olteț River Valley: A, the mandible VGr-2435 of *Dama eurygonos* from Valea Grăunceanului: A, occlusion surface; B, side view; C, occlusion view of the upper tooth row FM-0092 of *Dama* sp. from Fântâna lui Mitilan.

Table 18. Measurements of upper cheek teeth of fallow deer from Fântâna lui Mitilan, Valea Grăunceanului and Upper Valdarno.

Measurements	<i>Dama</i> sp.	<i>Dama eurygonos</i>				
	FM-0092	VGr-2441	IGF-12496	IGF-2847	IGF-244	IGF-260 ♀
L P ² -M ³	83.3		78.2	81.0		72.2
L P ² -P ⁴	37.7		35.4	36.1		33.8
L M ¹ -M ³	47.7		48.0	47.7		46.3
P ² L	12.2					
P ² D	12.0					
P ³ L	12.5					
P ³ D	13.5					
P ⁴ L	10.0		11.7	11.0		10.3
P ⁴ D	15.5		13.3	14.9		14.3
M ³ L	15.9	16.0	17.5	18.1	15.8	15.3
M ³ D	18.5	17.7	18.1	17.7	17.7	17.7

Dama sp.

Site

Fântâna lui Mitilan.

Dentition

The complete cheek tooth row in the right maxilla FM.0092 is deeply worn (Figure 29-C). M¹ is worn to the roots and details of its morphology and measurements are unavailable. M² and M³ are supplemented with well-developed basal pillars. The lingual walls of P² and P³ have vertical groves. The angle between the lingual rib of the protocone and the rib of the paracone on M³ is 37°. This character of the specimen under study is similar to that of *D. eurygonos* from Upper Valdarno (Croitor 2006a). The fallow deer from Fântâna lui Mitilan is slightly larger than *D. eurygonos*

(Table 18) and falls within the size variation range of *D. vallonnetensis* from Untermassfeld reported by Kahlke (1997).

Genus *Praemegaceros* Portis, 1920 Subgenus *Praemegaceros* Portis, 1920

Praemegaceros (Praemegaceros) obscurus (Azzaroli, 1953)

Site

La Baltini Valley (Olteț River Valley).

Antler

The proximal shed antler fragment Olt.0012 is characterised by a strong basal tine characteristic of *P. obscurus* that is situated close to the burr and a very obtuse first ramification angle (Figure 30). The burr is completely removed by weathering and erosion. The antler beam is sloped caudally immediately

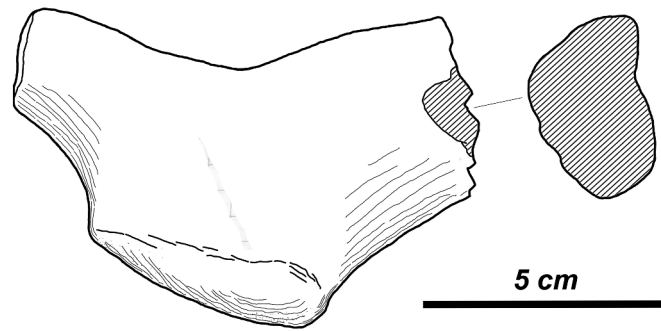


Figure 30. The proximal fragment of antler OLT-0012 of *Praemegaceros obscurus* from La Baltini Valley: the side view and cross-section of the preserved part of beam.

from the burr. The antler base is compressed from the sides (DAP, 53.0 mm; DLM, 35.0 mm). The beam cross section is irregular with a longitudinal groove on its lateral side. The beam circumference above the basal ramification is 111 mm. The specimen from La Baltini Valley is quite small compared to the samples of *P. obscurus* from Rotbav Silverstu (Rădulescu and Samson 1967), Salcia (Abbazzi et al. 1999) and Izvoru (Rădulescu and Samson 1986).

Praemegaceros (Praemegaceros) cf. mosbachensis Soergel, 1927

Sites

Homorâncea (Olteț River Valley), Fântâna lui Mitilan (upper level), Valea Grăunceanului (?).

Antlers

Two proximal shed antler fragments Olt.0042 from Homorâncea and FM.0024 from the upper level of Fântâna lui Mitilan are distinguished from the typical *P. obscurus* by their smaller size (DAP and DLM of the antler base are 59.0 by 48.5 mm and 63.0 by 49.2 mm, respectively), a strong reduction of the basal tine, which is present as a small vestige, and by the pronounced anteroposterior compression of the antler beam (51.0 by 38.3 mm and 47.5 by

40 mm; measurements are taken below the second tine). The lateral longitudinal groove between the basal vestigial tine and the dorsal tine is not expressed. The second tine situated on the dorsal side of the beam ('outer tine' according to Azzaroli and Mazza 1993; 'dorsal tine' according to Croitor 2006b) is well-developed and curved towards the anterior. The dorsal tine fragment FM.0028 is quite small compared to the sample of *P. obscurus* from the Forest Bed formation (England). The circumference of the specimen from Fântâna lui Mitilan (110 mm) equals measurements of the smallest specimens M6309 and M6315 (NHML) from the Forest Bed Formation.

The proximal fragment of a juvenile shed antler VGr.0943 is believed to be from Valea Grăunceanului, but most probably, it comes from younger levels. The antler specimen is strongly worn and the antler's burr is completely removed by erosion. The antler beam is sloped backward immediately from the burr. The beam axis forms an angle of ca. 60° with the burr plane. The beam is compressed dorsoventrally and has an irregular egg-shaped transverse section. The basal tine is not developed. The dorsal tine is broken off.

Teeth

The left mandibular ramus fragment with P₂-P₄ FM.0136 (Figure 31) comes from the upper levels of Fântâna lui Mitilan



Figure 31. The fragment of left ramus of mandible FM-0136 of *Praemegaceros cf. mosbachensis* from the upper levels of Fântâna lui Mitilan: A, occlusion surface; B, side view.

Table 19. Lower premolar measurements of *Praemegaceros cf. mosbachensis* compared to *P. obscurus* from Farlădeni and *Praemegaceros* from the Tiraspol gravel.

site	ID	L P ₂	D P ₂	L P ₃	D P ₃	L P ₄	D P ₄
Fântâna lui Mitilan	FM-0136	16.3	9.6	18.0	12.2	19.4	12.7
Fântâna lui Mitilan	FM-0137					20.3	12.4
Fărlădeni	FRD-53/3					20.5	12.3
Tiraspol gravel	OGU-3807					22.8	14.6
Tiraspol gravel	MGRI-1391					23.0	15.6
Tiraspol gravel	SUC-3/24			21.6	12.0	21.4	13.3
Tiraspol gravel	TIR-1/343	18.8	11.7	23.1	14.0	24.3	15.5

and may be associated with the antler FM.0024 of *P. cf. mosbachensis*. Its teeth are at an intermediate wear stage. P₄ is characterised by an advanced stage of molarisation: the metaconid is extended mesiolingually and is fused with the paraconid, thus closing the trigonid valley. The isolated right P₄ FM-0137 is at a slightly more advanced wear stage and shows a similar morphology.

The total length of the premolar series of FM.0136 (55.4 mm) is somewhat smaller than in *P. obscurus* from Pietrafitta (61.3 mm) and *Praemegaceros verticornis* from the Tiraspol gravel (M = 60.5 mm, lim = 58.3–64.0 mm; n = 3) and falls within the range of variation of *P. obscurus* from Ceysaguet (M = 55.7 mm, lim = 54.2–57.2 mm; n = 4). Measurements of P₄ from FM are very close to those of the specimen from Fărlădeni, Moldova (Table 19).

Family Giraffidae Gray, 1821

Subfamily Palaeotraginae Pilgrim, 1911

Genus *Mitilanotherium* Samson and Rădulescu, 1966

Mitilanotherium inexpectatum Samson and Rădulescu, 1966

Sites

Fântâna lui Mitilan, Valea Grăunceanului.

Teeth

FM.0002 (see Figure 4 Terhune et al. 2020), a lightly worn M₃ preserving only the talonid from Fântâna lui Mitilan is the type specimen of the giraffid species *Mitilanotherium inexpectatum* Samson and Rădulescu, 1966. The species was diagnosed as having

Table 20. Measurements of postcranial specimens of *Mitilanotherium inexpectatum* from Valea Grăunceanului compared to specimens attributed to the species from Dafnero, Dmanisi, Fonelas, Sésklo, Vaterá and Volakas. Metapodial robusticity index = (Diaphysis DLM*100/Length). * – estimated measurement.

Measurements: Astragalus	VGr-0967	VGr-2380	Sésklo Σ-1124	Vaterá PO 508 F			
Lateral L	83.9	84.4	82.8				
Medial L	80.3	75.2					
D	54.0	54.0	52.5	50.6			
Measurements: Metacarpal	VGr-0972	VGr-0973	Dmanisi specimens	Fonelas FP1-2002-1108	Volakas		
L*	400	400		400	410		
Proximal DAP	47.1	55.1	47, 48	44.5			
Proximal DLM	72	79.2	67.5, 73	72.4	73.5		
Robusticity*	9.25	9.75		9.75	9.63		
Measurements: Metatarsal	VGr-0970	VGr-0971	Dafnero DFN-68	Fonelas FP1-2001-0152	Dmanisi specimen	Sésklo Σ-58	
L*	422		443.1	491	460		
Proximal DAP	59.3	59.2	56.6	61.5	58	55.5	
Proximal DLM	60.7	58.5	56	65.7	60	59	
Robusticity*	8.3		12.1	6.7	7.4		
Measurements: Prox. Phalanges	VGr-0956	VGr-0957	VGr- 2169	Fonelas FP1-2001-0145	Fonelas FP1-2001-0146	Vaterá PO 061 F	Volakas
L	92.6	93.2	101.4	101.6	107.6	98.8	91.6
Proximal DAP	40.5	42.1	38.0	40.4	41.1	37.0	28.0
Proximal DLM	33.9	34.6	36.5	31.9	38.7	33.8	34.2
Distal DAP	23.5	23.9	23.8	24.8	30.5	27.2	26.5
Distal DLM	25.7	29.9	27.7	26.8	30.1	27.0	28.4
Measurements: Distal tibia	VGr-0967		Dafnero DFN-150	Sésklo Σ-50			
DAP	58.9		60.5	50.0			
DLM	67.2		67.9	69.0			

an elongated talonid (Samson and Rădulescu 1966) and compared to both *G. stillei* (Robinson 2011; Geraads et al. 2013) and the 'large morph' *Palaeotragus* specimens from Küçükçekmece, Maragheh, Pentalophos, Ravin de la Pluie and Xirochori (Erdbrink 1978; Kostopoulos and Saraç 2005; Kostopoulos and Sen 2016; Laskos and Kostopoulos 2022), the type specimen is elongated based on its estimated total length (39.0 mm; Samson and Rădulescu 1966) relative to its breadth (18.3 mm). *G. stillei* has shorter M_3 s of similar breadth to the type specimen while large *Palaeotragus* specimens have M_3 s that are similar in length but are, on average, 10% narrower. A more complete M_3 in a giraffid mandibular fragment from the Early Pleistocene site of Tsiotra Vryssi, Greece (Konidaris et al. 2015), is also unusually elongated (46.1 mm) relative to its breadth (19.8 mm) compared to similarly sized *Giraffa* and *Palaeotragus* specimens. Although the authors did not attribute the specimen to species it seems plausible that it could be ascribed to *Mitilanotherium*. The lingual rib on the entoconid of the type specimen is weakly developed as in some larger *Palaeotragus* specimens (Erdbrink 1978; Kostopoulos and Sen 2016). Its third lobe is small and lacks the bicuspid hypoconulid that characterises some *Palaeotragus* specimens (Kostopoulos and Saraç 2005; Kostopoulos 2009). Samson and Rădulescu (1966) described the tooth as mesodont, but Geraads (1998) correctly notes that it is actually relatively hypsodont compared to extant *Giraffa*. There is a small entostylid situated between the entoconid and hypoconulid, which has also been documented on a number of smaller African Plio-Pleistocene *Giraffa* specimens, being especially common on *G. pygmaea* specimens (Harris 1991; Robinson 2011), and on some *Palaeotragus* specimens (Kostopoulos 2009; Kostopoulos and Sen 2016).

Postcranials

Other than the type specimen, all of the giraffid material identified thus far in the Olteț River Valley collections are postcrania recovered from the site of VGr. They are all podials, metapodials and phalanges, other than one distal tibia and a fibula. Given that the similarities in size and shape between these specimens and those attributed to *Mitilanotherium* from the sites of Dafnero, Sésklo, Vaterá and Volakas in Greece, Fonelas in Spain and Dmanisi in Georgia (Sickenberg 1967; De Vos et al. 2002; Kostopoulos and Athanassiou 2005; Garrido and Arribas 2008; Vekua et al. 2008; Athanassiou 2014), that the type specimen of *Mitilanotherium* was recovered from a nearby site, albeit later in time, and that there are no other giraffid taxa currently identified from Europe at this time we ascribe the VGr postcranial material to *Mitilanotherium inexpectatum* as Samson and Rădulescu (1966) and subsequent authors have done.

The tibia (VGr.0961) preserves the distal articular surface and approximately 2/3 of the shaft. The articular surface is similar morphologically and metrically to the *Mitilanotherium* specimen from Dafnero with both being antero-posteriorly longer and medio-laterally narrower than the specimen from Sésklo (Kostopoulos and Athanassiou 2005; Table 19), which is more similar in its dimensions to *Palaeotragus rouenii* specimens from Samos and Akkasdagi (Kostopoulos and Saraç 2005; Kostopoulos 2009; Spassov et al. 2019). The fibula (VGr.2289) is a well-preserved specimen that is similar in its maximum length and morphology to smaller specimens attributed to *G. stillei* (Robinson 2011).

Three giraffid metacarpals (VGr.0401, VGr.0972 and VGr.0973)¹ and two nearly complete left metatarsals (VGr.0970 and VGr.0971) have been identified in the collections from VGr. All of the metapodials are missing their distal epiphyses due to breakage, so their lengths can only be estimated. However, their

preserved dimensions match those of other specimens attributed to *Mitilanotherium* (Sickenberg 1967; Kostopoulos and Athanassiou 2005; Garrido and Arribas 2008; Vekua et al. 2008; Athanassiou 2014; Table 20). *Mitilanotherium* was diagnosed as having a metatarsal proximal articular surface that is longer in its transverse diameter than in its sagittal diameter (Samson and Rădulescu 1966; Garrido and Arribas 2008), but we found that there is variation in this index among the *Mitilanotherium* specimens (Table 20) and that the mean dimensions of the known specimens are similar to those of the *Palaeotragus coelophrys* specimens from Pentalophos (Laskos and Kostopoulos 2022). Although there is some damage to their proximal articular surfaces, the metatarsal specimens from VGr appear to be similar to the specimen from Fonelas and, even more so, to the specimen from Dafnero in having two large, crescent-shaped articular facets of similar size and shape that are separated by a deep synovial fossa (Kostopoulos and Athanassiou 2005; Garrido and Arribas 2008). The metapodials from VGr all have at least moderately deep posterior troughs with sharp margins extending most of the way down the bone like in most other *Mitilanotherium* specimens (but see Sickenberg 1967) and *P. rouenii* (Kostopoulos and Athanassiou 2005; Garrido and Arribas 2008; Athanassiou 2014; Rios et al. 2016; Xafis et al. 2019). This distinguishes their metacarpals from those of most other palaeotragines and giraffines, which have been described as having shallow and very shallow troughs, respectively (Solounias 2007). Similar to *Palaeotragus* and distinct from *Giraffa* the metacarpal medial and lateral epicondyles are asymmetrical in size and morphology with the medial side being smaller (Rios et al. 2016). As in *P. rouenii* and living giraffes (Rios et al. 2016), the lateral and medial epicondyles of the metatarsal are of similar shape and size.

Two astragali from the VGr collections can be identified as giraffids (VGr.0967 and VGr.2380). The distal end of VGr.0967 articulates well with a cubonavicular specimen from the collections (VGr.2290) suggesting that they may belong to the same individual. The Grăunceanu specimens are similar in overall size to specimens attributed to *Mitilanotherium* from Vaterá and Sésklo (De Vos et al. 2002; Kostopoulos and Athanassiou 2005; Table 19) and to those ascribed to larger *Palaeotragus* species (Kostopoulos 2009; Kostopoulos and Sen 2016). However, they are distinct from *Palaeotragus* and *Giraffa* in having a reduced inequality between the lateral and medial proximal ridges of the trochlea (Samson and Rădulescu 1966; Kostopoulos and Athanassiou 2005). The astragali are also different from those of most *Palaeotragus*, and more similar to *Giraffa*, in having a deep lateral notch between the head and trochlea of the astragalus, which has been argued to be the primitive condition for giraffids (Solounias and Danowitz 2016).

Four cubonavicular specimens from VGr can be identified as giraffids (VGr.0968, VGr.0969, VGr.2290 and VGr.2370). VGr.0968 articulates well with a fragmentary calcaneus specimen (VGr.2283) and it seems likely that they are from the same individual. *Mitilanotherium* was diagnosed as having postero-internally expanded cubonaviculars that are missing the insertion for the peroneus longus (Samson and Rădulescu 1966). However, it appears that either the depiction of the cubonavicular by Bolomey (1965) omitted this groove or Samson and Rădulescu (1966) misinterpreted the drawing because this groove is clearly present as Geraads (1998) suspected based on the morphology of the metatarsals. The cubonaviculars from VGr are similar in size to *G. stillei* specimens (Robinson 2011) and to a specimen from the Early

Pleistocene site of Mukhai II attributed to *P. priasovicus* (Amirkhanov et al. 2015).

Three proximal phalanges from VGr can be attributed to the Giraffidae (VGr.0956, VGr.0957 and VGr.2169), with two of them (VGr.0956 and VGr.2169) being derived from juveniles, possibly from the same individual. Similar to the proximal phalanx specimens attributed to *M. inexpectatum* from Vatera, Volakas and Fonelas (Sickenberg 1967; De Vos et al. 2002; Garrido and Arribas 2008), albeit not quite to the same degree, the phalanges from Grăunceanu are elongated and slender, with small articular surfaces relative to their lengths (Table 20) when compared with *G. stillei* (Robinson 2011). This feature is shared with *P. rouenii* specimens from Nikiti-2 but not specimens of the large morph of *Palaeotragus* from Küçükçekmece West, which have shorter phalanges but larger articular surfaces (Kostopoulos 2016; Kostopoulos and Sen 2016).

Discussion

Pachyrocata faunal turnover in the Dacian Basin

The ruminants from the Olteţ River Valley form two clearly distinct biochronological groups: the rather archaic and rich in species pre-*Pachyrocata* assemblage (*Pliotragus ardeus*, *Gazellospira torticornis*, *Bison* (*Eobison*) sp., *Alces* sp., *Rucervus radulescui*, *Eucladoceros dicranios*, *Eucladoceros ctenoides*, *Metacervoceros rhenanus*, *Dama eurygonos* and *Mitilanoherium inexpectatum*) and the geochronologically younger post-*Pachyrocata* assemblage (*Megalovis latifrons*, *Eucladoceros* sp., *Dama* sp., *Praemegaceros obscurus* and its specialised diminished form *Praemegaceros* cf. *mosbachensis* and *Mitilanoherium inexpectatum*) that evolved after the wolf/*Pachyrocata* faunal event. The most of fossil remains of the pre- and post-*Pachyrocata* assemblages come from VGr and FM, respectively, but also from several smaller coeval sites. Those two assemblages of ruminants represent a great interest from the palaeoecological and paleobiogeographic points of view since they reveal the climate and biogeographic shifts in the region during the early stages of the Late Villafranchian. Thus, we propose a detailed discussion of ecomorphology, evolution and biogeography of each ruminant species in order to reveal the paleoenvironmental changes that followed the above-mentioned faunal turnover in the area under study.

Pre-*Pachyrocata* event ruminants

Pliotragus ardeus

Pliotragus ardeus is the most common bovid in the Early Pleistocene of southern Romania. The taxonomy of *P. ardeus* and its systematic position remained uncertain for a very long time. Depéret (1884) described a braincase with proximal horn core parts and a fragment of the upper maxilla with a complete tooth row of a red-deer-sized bovid from the Pliocene of Perrier-Etouvaires (Auvergne, France) as *Antilope ardea*. Depéret (1884) also ascribed to this species a relatively long (270 mm) metacarpal that seems to be lost (Duvernois and Guerin 1989). According to Duvernois and Guerin (1989), the metacarpal mentioned by Depéret is too long for a caprine of such size and should be excluded from the species hypodigm. Schaub (1923) proposed to include *Antilope ardea* in the genus *Deperetia*. The description of *Deperetia* is supplemented with a brief definition based entirely on the braincase figured by Depéret (1884), Pl. 8, (Figure 1). Kretzoi (1941, p. 258) created the genus

Pliotragus as a substitute for *Deperetia* Schaub, 1923, which was occupied by the pectenid genus *Deperetia* Teppner, 1921. Schaub (1923) and Sokolov (1953) regarded *P. ardeus* as Bovidae *incertae sedis*. McKenna and Bell (1997) synonymised *Pliotragus* with *Megalovis* following the suggestion of Gentry (1970) of a possible synonymy of those two genera. In our opinion, both genus names should be maintained since their type species are distinguished by important cranial features that are regarded as diagnostic characteristics at the genus level (Sokolov 1953). The braincase of *Megalovis* is relatively short and little flexed, the horn cores are compressed from the sides and directed from the skull sideward and then upwards (Schaub 1943; Sokolov 1953). Unlike *Megalovis*, *P. ardeus* is characterised by a rather long and flexed braincase and short cone-shaped horn cores with circular or slightly oval cross-sections that form almost a right angle with the parietal surface of the braincase (Depéret 1884; Sokolov 1953). Crégut-Bonnouire (2007) included *Pliotragus* in the tribe Rupicaprini of the subfamily Caprinae and this viewpoint is followed in the present study. The palaeontological record of *P. ardeus* from the Early Pleistocene of Romania is the richest and most complete in Europe: fossil remains of this bovid come from several Late Villafranchian sites (La Pietriş, Irimeşti, VGr) and include fine cranial remains and complete postcranial bones (Bolomey 1965; Popescu 2004). Some of the postcranials ascribed by Bolomey (1965) to *P. ardeus* apparently do not belong to this species: a complete radius Gr.253/202 and a proximal radius Gr.203 (the material is stored in the Gorjului Museum of Târgu Jiu, Romania) are too robust and the measurements of their epiphyses rather correspond to an animal as heavy and large as *Bison*, while the complete radius is too long (499 mm) for such a heavy bovid. Most probably, the radii in question belong to a giraffid.

The biogeographic origin and phylogenetic relationships of *P. ardeus* have never been discussed before. *Capraoryx orientalis* Alekseeva, 1977 from the Late Villafranchian of Velyka Komyshevakhka (Kharkiv, Ukraine) seems to be closely related to *P. ardeus*. *Capraoryx orientalis* is characterised by relatively short, cone-shaped and gently curved horn-cores without torsion (Alekseeva 1977) as in *P. ardeus*. The position of the horn cores above the posterior third of the orbits is another character shared by *P. ardeus* and *C. orientalis*. Unlike *P. ardeus*, *C. orientalis* is characterised by stronger lateromedial compression of the horn cores, a character shared with *Soergelia* from Dmanisi and Venta Micena, and a very slight divergence of the horn cores, a character shared with *Procamptoceras brivatense*.

P. ardeus appeared in the European palaeontological record much earlier than *Megalovis*, being found in the Perrier-Etouvaires faunal assemblage, and it is generally less specialised than *Megalovis*. The shape of the horn cores in *P. ardeus* represents the most primitive ecomorphological state for the Rupicaprini, which is also found in modern *Capricornis* (Masini and Lovari 1988).

Some morphological features of *P. ardeus* from VGr (such as the strong development of the posterior lobe of P₄ and the presence of basal columns on the lower molars) may be regarded as a primitive morphological condition compared to *Pliotragus* from Sénéze (Duvernois and Guerin 1989), (Figure 3–3). Possibly, we are dealing here with a biogeographic phenomenon that may be formulated as the following rule: ruminant populations show more advanced morphological features with increasing geographic distance from their centre of origin (see, for instance, the case of the moose described by Nikolskiy and Boeskorov 2011). Generally, *P. ardeus* from VGr and Sénéze show different combinations of advanced and primitive dental features that may indicate an independent parallel evolutionary development of Southeastern and Western European populations. However, the taxonomic significance of the differences

in premolar morphology is not clear, since individual variation in the dental morphology of *P. ardeus* is poorly known.

The craniodental morphology suggests that *P. ardeus* was not a browser. The relatively long diastema and angular parts of the mandible are rather characteristic of grazing ruminants (Janis 1990), while the obtuse angle of the occipital and parietal planes (Bolomey 1965), p. 1 (Figure 2) may suggest that *P. ardeus* was an intermediate- or low-level feeder. This conclusion is derived from the fact that an acute occipito-parietal angle, according to our observations, is characteristic of high-level browsers, such as *Giraffa camelopardalis* and *Alces alces*.

The proportions of postcranial skeleton in *P. ardeus* generally are typical for a mountain climber (Egorov 1955; Köhler 1993); however, the metapodials are relatively longer and more slender than in most mountain climbers. Unlike *Gallogoral meneghinii*, which shows an advanced specialisation for climbing in rocky environments, *P. ardeus* is characterised by long limb bones and relatively longer metacarpals and metatarsals. The estimated body mass of *P. ardeus* based on dental measurements provided by Depéret (1884) was ca. 200 kg, too heavy for an effective mountain climber (Croitor 2016c). The peculiar limb proportions and morphology of *P. ardeus* represent a combination of the morphological features of a mountain climber with cursorial locomotion specialisation. Possibly, this unusual eco-morphological type resulted from a relatively early evolutionary shift from mountain habitats to plains triggered by the mid-Pliocene cold phase. One can assume that this climate shift allowed the initially cold-adapted mountain climber *Pliotragus* to occupy lowlands and to replace Pliocene warm-loving species. The rather primitively short and slightly bowed horn-cores developed in both sexes represent an offensive weapon capable of inflicting damage. Such an effective weapon in bovids usually serves for resource and territory defence (Estes 1974; Köhler 1993).

Gazellospira torticornis

This is a quite large-sized bovid (the estimated body mass is ca. 200–230 kg) with the earliest specimens from Western Europe described from the Early Villafranchian (Depéret 1884), although the oldest *Gazellospira* are reported from the Pliocene of Eastern Europe (Hermier et al. 2020). According to Titov (2008), the Asian counterpart species *Gazellospira gromovae* Dmitrieva, 1977 is present in fauna from Liventsovka, Russia (Azov Sea Area), and Bolgrad, Ukraine (northwestern Pontic Area); however, Vislobokova et al. (2020) did not confirm the presence of *G. gromovae* in the Ponto-Mediterranean area. Hermier et al. (2020) placed *Gazellospira* from Liventsovka closer to *G. torticornis* and included in the genus *Gazellospira* the poorly understood ‘*Antilospira?*’ *zdanskyi* Teilhard de Chardin and Trassaert, 1938 from the Late Tertiary of China as a senior synonym of *G. gromovae*. Therefore, the geographic distribution of *Gazellospira* with species *G. zdanskyi* (Teilhard de Chardin and Trassaert, 1938) and *G. torticornis* (Depéret, 1884) fringes the Alpine-Himalayan mountain belt from the north across the entire Eurasian continent. Such a latitudinal area of distribution suggests that *Gazellospira* was adapted to a rather dry and warm climate of the Mediterranean type (Athanasios 2005; Demirel and Mayda 2014).

According to Hermier et al. (2020), the Pontic area was the centre of the *Gazellospira* lineage evolution. Gentry (1971) indicates a possible phylogenetic relationship between *Gazellospira* and the late Miocene *Protragelaphus*. The genus *Protragelaphus* is known from the Late Miocene of Pikermi (Greece), Grebeniki (Ukraine) and Taraclia (Moldova) (Sokolov 1953), thus also suggesting the Ponto-Mediterranean origin of *Gazellospira*. The

paleoenvironments of *Protragelaphus* from Samos and Pikermi, according to Solounias and Dawson-Saunders (1988), were dominated by mixed non-canopy forming woodlands and forest with a minor sclerophyllous component. The palaeobotanic data are supported by the functional morphology of bovids from Samos and Pikermi, which indicates an adaptation to browsing and mixed feeding (Solounias and Dawson-Saunders 1988; Solounias and Moelleken 1999). The further evolution of *Gazellospira* could be linked to the forested humid biotopes from the Carpathian area and Balkans reported by Eronen and Rook (2004) and Fortelius et al. (2006). The large fossa praeorbitalis that we observed in the cranial fragment of *G. torticornis* from Sénéze (FSL211708, Claude Bernard University of Lyon) indicates territorial and social marking behaviour in wooded/forest environments similar to that in modern cervids. The deep fossa praeorbitalis is also known in *Protragelaphus* (Sokolov 1953), thus suggesting that this specific adaptation to forested conditions may represent a rather old evolutionary acquisition. The mesowear analysis carried out by Strani et al. (2015) indicates that *G. torticornis* from Costa San Giacomo inhabited closed forests, thus supporting the assumed ecological relationship of this bovid with forested biotopes.

The comparatively long metapodials (‘cervid-like’, according to Athanassiou 2005) define *G. torticornis* as a good runner adapted to wooded plains with insignificant obstacles like low shrubs (Gambarian 1972). The metatarsal diaphyses that are strongly compressed from the sides with a symmetric cross-section indicates an old adaptation to endurance running, since the longest axis of the diaphysis cross-section coincides with parasagittal movement of the limbs (Korotkevich 1988). According to Korotkevich (1988), forest and mountain dwellers, metapodials of which experience multiaxial bending forces, have relatively broader diaphysis with asymmetric cross-sections. Thus, *G. torticornis* is characterised by a combination of adaptations to endurance running in plains with light cover and social adaptations to intraspecific resource partitioning. The type of vegetation, apparently, did not represent an important ecological limiting factor, since *G. torticornis* could easily switch from Mediterranean forests, as, for instance, in the fauna from Costa San Giacomo, the Italian Peninsula (Strani et al. 2015), to open plains with light tree cover (Rivals and Athanassiou 2008; Hermier et al. 2020). Correspondingly, the paleodiet of *G. torticornis* ranged from browsing on leaves to being a mixed feeder and grazer (Rivals and Athanassiou 2008; Strani et al. 2015; Hermier et al. 2020) and the species was capable of switching to browse depending on the availability of better-quality forage resources (Strani et al. 2018). Mesodont cheek teeth (Garrido 2008a; Sianis et al. 2022) suggests that *G. torticornis* was not a specialised grazer. Nonetheless, the area of distribution suggests that *G. torticornis* was a temperature-sensitive species.

Bison

Two species *Bison tamanensis* Verestchagin, 1957 and *Bison sukhovi* Alekseeva, 1967 from the Early/Middle and Early Pleistocene of southeastern Europe are based on poorly preserved cranial and horn core fragments (Croitor 2016b). Kostopoulos et al. (2018) noted a series of advanced features, such as a less expressed skull constriction behind the horn-cores and a shorter corneal process that distinguish *B. (E.) tamanensis* from *B. (E.) palaeosinensis* (the type species of the subfamily *Eobison*), and regarded the Tamanian bison as *species inquirenda*.

Bukhsianidze (2005) included the Late Villafranchian species *Dmanisibos georgicus* Burchak-Abramovich and Vekua, 1994 from Dmanisi in *B. (Eobison)*, since the Georgian species shows most of the diagnostic features of the subgenus *Eobison*. Kostopoulos et al.

(2018) regard *B. (E.) georgicus* as less derived than *B. (E.) tamanensis* and showing a greater affinity with *B. (E.) palaeosinensis*.

Masini et al. (2013) reported on the small form (ca. 280 kg according to Croitor and Brugal 2007 and 380 kg according to; Masini et al. 2013) of primitive bison *B. (E.) degiulii* from the latest Villafranchian – Early Galerian of the southern part of the Italian Peninsula. According to Bukhsianidze (2005) and Kostopoulos et al. (2018), *B. (E.) degiulii* is quite advanced and should be included in the subgenus *Bison* (*Bison*), since its specialised cranial morphology is closer to the advanced type of bison. Croitor and Brugal (2007) supposed that *B. (E.) degiulii* could be an endemic dwarfed form that evolved along with the moderately dwarfed fallow deer from Pirro Nord.

Recently Kostopoulos et al. (2018) proposed abandoning the concept of the subgenus *Eobison* since part of the species ascribed to *Eobison* does not fully comply with the taxon definition and shows some advanced features of *Bison sensu stricto*. This viewpoint is worthy of attention, since Flerov (1972) who described *Eobison* certainly followed the taxonomic model proposed by Skinner and Kaisen (1947) who divided *Bison* into multiple subgenera – most of them now abandoned – and included *B. palaeosinensis* and *B. sivalensis* into an ‘unnamed primitive subgenus’ (Skinner and Kaisen 1947, p. 212). However, the new taxonomic concept of early Eurasian *Bison* requires a better understanding of the early evolution and taxonomy of the genus. Those questions are outside of the scope of the present study, therefore we keep using the subgenus *Eobison* in order to designate the primitive Early Pleistocene *Bison* forms.

Kostopoulos et al. (2018) described a comparatively larger (ca. 550 kg according to Maniakas and Kostopoulos 2017a) primitive bison from the Early Pleistocene of the Mygdonia basin (Greece) as *B. (Bison) cf. degiulii* (Masini et al. 2013). According to Kostopoulos et al. (2018), the primitive bison from the Mygdonia basin shares with *B. degiulii* some cranial features, including convex and pneumatized frontal bones. However, the material from the Mygdonia basin does not contain fully grown mature cranial specimens; therefore, the morphological record of the Greek bison remains incomplete. Maniakas and Kostopoulos (2017a, b) define the bison from the Early Pleistocene of the Mygdonia basin as a rather small-sized (similar to modern *B. bison*) open-landscape dweller with grazing habits, stressing, however, the generally flexible and opportunistic ecology of early representatives of the genus *Bison*.

According to Kostopoulos et al. (2018), the earliest bison dispersed into the southern Balkans 1.7–1.5 My ago. A similar chronological timeframe (1.8–1.5 Ma) is reported for *B. (Eobison) sp.* from Taurida Cave, Crimea (Lopatin et al. 2019). The remains of *Bison* from Valea Grăunceanului indicate a somewhat earlier presence of this bovid lineage in southeastern Europe that took place before the *Pachyrocuta* event. The biogeographic origin of primitive bison from southeastern Europe remains uncertain, since its relationship with *B. (E.) sivalensis* from the Indian Subcontinent is not clear.

Alces

Pleistocene moose are represented by a comparatively small evolutionary radiation with few species, which had a vast distribution in the temperate latitudes of Eurasia. The Pleistocene forms of moose often are regarded as ‘chronospecies’ and placed in different genera: *Libralces* Azzaroli, 1952 with the type species *Libralces gallicus* Azzaroli, 1952 from the Early Pleistocene of Sènèze; and *Praealces*; Portis, 1920 with the type species *Cervus latifrons* Johnson, 1874 from the Pleistocene of the Cromer Forest Bed Formation (Portis 1920; Rădulescu and Samson 1990; Abbazzi et al. 1999). The species and, correspondingly, genera are mostly

distinguished by their body size and the relative length of their antler beams (Lister 1987; Abbazzi et al. 1999). According to this taxonomic model, the taxonomic definition of the third species, *Alces carnutorum* (Laugel 1862), remains unclear, since the only available diagnostic character of this species is the size of its teeth being intermediate between *gallicus* and *latifrons*, while antler remains securely associated with dental remains unknown (Heintz and Poplin 1980). Azzaroli (1985) proposed to include all fossil moose from Eurasia in the genus *Cervalces* Scott, 1885 based on the endemic North American species *Cervalces scotti* Lydekker, 1898. The difference in occipital shape between *A. gallicus* (broad and low occiput) and *A. alces* (high and narrow occiput) considered by Azzaroli (1952) as a taxonomically meaningful feature rather represents an adaptation to their feeding level: the high and narrow occiput in modern moose resembles the shape of this part of the skull in such high-level browsers as modern Giraffidae. *C. scotti* from the Late Pleistocene of Nearctic is a specialised cervid that evolved in biogeographic isolation from the Old World elks. The combination of the archaic moose of the Old World and the endemic specialised North American species into one genus raises questions. Therefore, following Heintz and Poplin (1980) and Lister (1987, 1993), we include all Eurasian Pleistocene moose forms in the genus *Alces*.

The oldest moose-like deer is reported from the Pliocene of the Baikal Area (Vislobokova et al. 1995), thus suggesting an East Asian origin for *Alces*. By the Late Villafranchian, *Alces gallicus* achieved a vast distribution ranging from central Asia to Western Europe (Vislobokova 1986, 1990). The arrival of ancient moose in Europe has not been regarded as an important dispersal event; however, the occurrence of *A. gallicus* in Sènèze has palaeobiologic and palaeoecologic importance, since this is the first occurrence of a large-sized cervid (ca. 400 kg) with palmed antlers in Western Eurasia (Brugal and Croitor 2007). The palaeontological record has never yielded large samples of this species, a fact that was interpreted by Breda (2008) as evidence that *A. gallicus* was not a gregarious species. The combination of morphological features of *A. gallicus* is puzzling. The exceptionally large antler span and the development of distal palmations would suggest that *A. gallicus* was not a forest dweller because its wide antlers would have hampered movements (Lister 1987). The adaptation to open landscapes may be confirmed by the relatively long metapodials of *A. gallicus* (Breda 2008). Thus, Kahlke (2006) assumed that *A. gallicus* inhabited temperate steppes. However, the spherical shape of the femoral head and brachydonty of the molars conflict with the presumed adaptation of the ancient moose to open landscapes (Breda 2008). According to Breda (2008), *A. gallicus* inhabited open woodlands and gallery forests; however, this assumption is still contradicted by some evidence. The low and broad occiput in *A. gallicus* suggests that this species, unlike *A. alces*, was not a specialised high-level browser. The exceptionally long third phalanges doubtless indicate an adaptation of *A. gallicus* to marshy soil surfaces as in modern *A. alces* (Breda 2008; Curran 2012). We suggest that the combination of antler, dental and post-cranial characters of *A. gallicus* represent a specific adaptation to flooded marshy meadows and river valley grasslands. This interpretation of morpho-functional characteristics may explain the odd combination of open landscape features with brachydonty, the adaptation to multi-axial movements of the hip joint and the long, wide spreading third phalanxes.

The Early Pleistocene of the Dacian Basin has yielded quite scarce remains of the archaic moose. The best specimen confirming the presence of *Alces gallicus* in the Dacian Basin is a shed almost complete antler from the Early Pleistocene deposits of Prundu (Giurgiu district, Romania) discovered in association with *Mammuthus meridionalis* (Apostol 1972). Rădulescu and Samson

(1990) reported the presence of *Alces gallicus* (= *Praealces gallicus*) from the Tetoiu middle faunal horizon of Valea Mijlociei. Popescu (2004) reported *A. gallicus* in the composition of the Early Pleistocene fauna of Leu, Oltenia. Although the moose from VGr is represented by a small and imperfect sample (the unusual antler and astragali) that does not provide sufficient arguments for species definition, it is most probably close to or conspecific with *A. gallicus*.

The geographical distribution of Early Pleistocene moose in Western Eurasia is characterised by some interesting features that may be meaningful from a palaeoecological point of view. For example, *A. gallicus* is completely absent in the Iberian and Italian peninsulas, however, moose remains are reported from the important palaeoanthropological site of Dmanisi (Bukhsianidze 2016), suggesting a biogeographic connection of Transcaucasia with the temperate latitudes of Eurasia. A poorly preserved fragment of a quite thin antler beam (the antler diameter is 28.4 mm) from Denizli (Turkey) is reported by Boulbes et al. (2014) as *Cervalces (Libralces) ex gr. minor-gallicus*. The presence of a dwarfed moose in the Mediterranean environment is exceptional and very curious; however, a well-documented confirmation of this identification is needed.

Eucladoceros dicranios

Several species and subspecies of *Eucladoceros* with peculiar dichotomously branched antlers are described from the Early Pleistocene of Europe: *E. dicranios* (Nesti, 1841) from Upper Valdarno (Italy); *E. sedgwickii* Falconer, 1868 from Bacton, Norfolk (England); and *E. dicranios tanaitensis* Bajgusheva and Titov, 2013 from Liventsovka (Russia). According to De Vos et al. (1995), *E. sedgwickii* and *E. dicranios* are synonymous. If one applies the taxonomic concept proposed by Bajgusheva and Titov (2013), *E. dicranios* from Upper Valdarno should be regarded as the nominotypical subspecies *E. dicranios dicranios*, while the deer from Bacton becomes *E. dicranios sedgwickii*. The differences between *E. dicranios dicranios* and *E. dicranios tanaitensis* concern some morphological details of the crown tines that actually may represent individual variants. *E. dicranios sedgwickii* is the most specialised form, distinguished from both *E. dicranios dicranios* and *E. dicranios tanaitensis* by a very high position of the first ramification and the loss of an accessory prong in the area of the first ramification.

The shape of antler remains from VGr corresponds to the antlers of *E. dicranios dicranios* and *E. dicranios tanaiticus*. The diagnostic characters proposed by Bajgusheva and Titov (2013) to distinguish between those two subspecies cannot be applied to the material from VGr, since the available material did not preserve crown tines.

Azzaroli and Mazza (1992) suggest that the richly branched antlers of *E. dicranios* could not be used in intraspecific combats because of the apparent fragility of numerous small branches and the high risk that fighting males will entangle in an inextricable grip. Therefore, according to the cited authors, the antlers were used by *E. dicranios* for ritualised social display. Azzaroli and Mazza (1992) proposed an artistic reconstruction of the *E. dicranios* environment that resembles a thin forest with a disrupted canopy. The earliest remains of *E. dicranios* from Liventsovka indicate the East European origin of this species (Bajgusheva and Titov 2013). According to Croitor and Popescu (2011), the dense mountain forests of the Dinaric Alps represented an effective biogeographic obstacle for *E. dicranios*, a fact that explains the earlier occurrence of this species in the Dacian Basin (before the *Pachycrocuta* event), but its quite late dispersal into the Italian Peninsula: remains of *E. dicranios* on the Italian peninsula come from the Tasso Faunal Unit, well after the *Pachycrocuta* event (Gliozzi et al. 1997).

E. dicranios is absent in the palaeontological record of the Iberian Peninsula and still unknown from the southern part of the Balkans.

Eucladoceros ctenoides

The Early Pleistocene palaeontological record of Western Europe has yielded abundant remains of a red-deer-sized *Eucladoceros* with a specific comb-like shape of the antlers. Several well-represented samples from Western Europe are described under different species names: *Eucladoceros ctenoides* (Nesti, 1841) from the Upper Valdarno (Italy), *E. darestei* (Depéret, 1931) and *E. senezensis* (Depéret and Mayet, 1910) from Senezé (France), *E. tetraceros* (Dawkins, 1878) from Peyrolles (France), *E. ertbornii* (Dubois, 1907) from Campine (Belgium), *E. falconeri* (Dawkins, 1868) from the Red Crag and Norwich Crag (England) and *E. teguliensis* (Dubois, 1904) from Tegelen (the Netherlands) (De Vos et al. 1995). The distinction between most of those species lies in minor details of antler morphology, such as crown tine bending and the relative length of the antler crown segment. Azzaroli and Mazza (1992) regarded *E. falconeri* as the earliest and a quite small-sized representative of *Eucladoceros*. Actually, the holotype of *E. falconeri* is a very young antler, a fact that explains its small size. The sample from the type locality of Norwich Crag also contains a fully grown antler M15696 (NHML) that falls within the size range of *Eucladoceros* from Senezé and Saint-Vallier, suggesting that we are dealing with the same cervid form. According to De Vos et al. (1995), all *Eucladoceros* with simple comb-like antlers are junior synonyms of *E. ctenoides* (Nesti, 1841) and this viewpoint has never been contested. Nonetheless, the morphological distinctions of the antlers of some samples have ecological and evolutionary significance; therefore, the local and chronological forms of *E. ctenoides* are maintained as subspecies (2005; Croitor 2014; Curran 2015). The type specimen of *E. falconeri*, although incomplete, shows the morphological peculiarities that make this form resemble the samples from Senezé, Saint-Vallier and Tegelen: a rather high position of the first tine, a long antler beam segment between the first ramification and the crown part and a strong accessory prong situated at a certain distance from the first tine. Therefore, *E. ctenoides falconeri* (Dawkins, 1868) is the senior synonym of *E. ctenoides darestei* (Depéret, 1931), *E. ctenoides senezensis* (Depéret and Mayet, 1910) and *E. ctenoides teguliensis* (Dubois, 1904). The morphological characteristics listed above are also present in the antler remains of *E. ctenoides* from VGr. Therefore, *E. ctenoides falconeri* from VGr is the first record of this cervid form in Eastern Europe based on the clearly diagnostic antler material.

The origin of *Eucladoceros* has been suggested as being in the Early Pliocene of East Asia (Yushe Basin, China) where the earliest species of the genus, *E. proboulei*, was described (Dong and Ye 1996). The westward dispersal of the genus *Eucladoceros* took place during the Middle Villafranchian and coincided with the onset of 40 kyr glacial cycles (Brugal and Croitor 2007). Unlike *E. dicranios*, the distribution of *E. ctenoides* is mostly restricted to Western Europe, suggesting more stenobiont ecological requirements for the latter species. According to Vervoort-Kerkhoff and Kolfshoten (1987), *E. ctenoides falconeri* from Tegelen inhabited dense, humid forests. This assumption is supported by the mesowear and ecomorphological study of Valli and Palombo (2005) that revealed the predominately browsing habits of *E. ctenoides falconeri* from Saint-Vallier and Senezé. On the other hand, Berlioz et al. (2018) reported a grazing signal in dental microwear of *E. ctenoides* from those sites and questioned the reliability of the results obtained by Valli and Palombo (2005). The apparent contradiction of the obtained results in this case should rather be regarded as complimentary information, since the microwear, mesowear and

functional morphology data provide palaeoecological information at the different scales: seasonal, functional-physiological and evolutionary. One can expect a certain discrepancy of palaeoecological signals at different scales in conditions of seasonal or changing climate. In order to have a correct interpretation of the data, it is important to know the taphonomic context of the microwear study carried out by Berlioz et al. (2018), namely evidence of seasonality. Interestingly enough, almost all cranial and antler specimens of *E. ctenoides* from S n ze described and figured by Heintz (1970) (with exception of a single fragment of shed antler) represent antlers attached to the pedicles, suggesting that the remains of *E. ctenoides* from S n ze were accumulated during a certain (autumn-winter?) season. It is highly probable that this circumstance is mirrored by the dental microwear signal obtained by Berlioz et al. (2018) and provides evidence of a seasonal shift in the *E. ctenoides* diet (Curran et al. 2021). The mesowear signal of *E. ctenoides* from Ceyssaguet (France) indicates abrasion dominated mixed feeding in conditions of accentuated seasonality shortly before the extinction of this species (Kaiser and Croitor 2004).

The presence in a limited area of Western Europe of several subspecies with well-distinguished antler shapes provides evidence that *Eucladoceros* populations were exposed to permanent multidirectional selection pressures. *E. ctenoides falconeri* shows the most derived forest adaptations among the comb-antlered deer: its antlers show an advanced specialisation in the elongated proximal portion of the antler and the relatively shortened crown part. The antler crown is rather compact due to the crown tines being bowed medially and anteriorly. The occurrence of rare remains of *E. ctenoides falconeri* in the fauna from VGr, most probably, is related to Carpathian mountain forests and suggests a biogeographic contact with the Western European paleobiogeographic zone.

Rucervus (Arvernoceros) radulescui

The remains of this species in the fauna from VGr are abundant. Its limb bones and dentition show a great biometric similarity to *Eucladoceros* from Western Europe, a circumstance that caused the initial attribution of this cervid to *Eucladoceros* (R dulescu and Samson 1990). The main evidence of the quite distant phylogenetic position of *R. radulescui* from *Eucladoceros* is provided by its antler morphology: the antlers of *R. radulescui* show a different antler bauplan characterised by the development of crown tines on the posterior side of the antler beam. This difference in antler construction is important and suggests a long evolutionary path distinct from *Eucladoceros* and a closer phylogenetic relationship with modern *Rucervus duvaucelii* (Croitor 2018b). Unlike *R. duvaucelii*, the crown tines in *R. radulescui* merged into a small distal palmation. The antler shape in *R. radulescui* is very similar to that of *R. (Arvernoceros) ardei* from the Pliocene of Europe, suggesting a direct phyletic relationship between those two species. *R. radulescui* is distinguished from *R. ardei* by its larger body size and the loss of the accessory prong of the basal tine. The additional material from VGr described in the present study provides evidence that the antlers of *R. radulescui* may develop an atavistic accessory prong on the basal tine, but this morphological variant is observed on only one antler specimen. In very large antlers, the basal tine is characterised by moderate flattening in its middle portion that is reminiscent of the flattened basal tine in *R. ardei*.

The general morphology and proportions of the dentition and limbs of *R. radulescui* and *E. ctenoides* differ very little, suggesting that those two species evolved in the same adaptive zone and share similar eco-physiological and locomotory adaptations. Therefore, competition between these two cervids for the same ecological

resources is highly probable. Possibly, this ecological incompatibility was one of the causes of the replacement of *R. ardei* by *E. ctenoides* in Western Europe. The distribution of *R. radulescui* in the Dacian Basin and the North Pontic Area has a rather refugial character similar to that of *Haploidoceros mediterraneus*, another Pleistocene endemic descent of *R. ardei* that survived in the Iberian Peninsula (Croitor et al. 2020). The survival of Pleistocene forms related to *R. ardei* in southern refugia is evidence that *Rucervus (Arvernoceros)* remained a warm-loving cervid lineage that could not tolerate the cooler climate and accentuated seasonality. Apparently, *Eucladoceros*, which dispersed into Western Europe simultaneously with the establishment of 40 ky Milankovich cycles, had certain advantages in the new climate conditions. Generally, the antlers of *R. radulescui* maintain the bauplan characteristic of large subtropical/tropical cervids, which do not evolve the trez (middle) tine. The trez tine and its analogies are characteristic of practically all Palearctic representatives of the subfamily Cervinae (Croitor 2020). This tine represents an additional level of protection during combat, a sort of evolutionary compensation for the excessive male mortality after the rutting season during winters (*ibidem*). The trez tine is never present in cervids from subtropical and tropical latitudes (*Panolia eldii*, *Rucervus duvaucelii*, etc.). Therefore, the absence of a middle antler tine in *R. radulescui* characterises this species as a preglacial faunal holdover that survived in southeastern Europe. Its palmed antlers suggest that this cervid inhabited more or less open environments, such as sparse woodlands with discontinuous canopy where the antler palmations served as a visual interspecific signal.

The antler morphology corresponds perfectly to the morpho-functional adaptations of *R. radulescui* postcranials. The blocky femoral head in *R. radulescui* is reminiscent of the peculiar shape of this feature in *Ozotoceros bezoarticus*, the Pampas deer, which inhabits grasslands in South America, and other open adapted artiodactyls (Curran 2015). This observation may be supported by the anteroposterior extension of the metatarsal diaphysis in *R. radulescui*, which may be interpreted as a biomechanical adaptation to parasagittal bending forces during fast running in more or less open landscapes. The morphofunctional analysis of *E. ctenoides* postcranials from Saint-Vallier and S n ze and *R. radulescui* from VGr demonstrate their adaptations to different types of paleohabitats. *Eucladoceros* from Western Europe shows adaptations to intermediate wooded paleohabitats, while *R. radulescui* was more open adapted in drier conditions (Curran 2015; Curran et al. 2021). Therefore, the adaptation to different habitats ensured ecological resource partitioning between *E. ctenoides* and *R. radulescui* that are found together in VGr. The combination of mesowear, microwear and isotope analysis of ruminant dental remains from VGr (mostly *R. radulescui*) revealed a combination of paleodiet signals (browsing mesowear signal and grazing microwear signal) suggesting a habitual browsing diet and exposure to seasonal droughts during winter, with a switch to a grazing diet (Curran et al. 2021).

Berlioz et al. (2018) consider the Early Pleistocene remains of large cervids from Western and Southern Europe as one ecologically flexible species similar in its ecological habits to modern *Cervus elaphus*. However, the extrapolation of palaeoecological and biogeographical features of *Cervus elaphus* to the archaic Villafranchian cervid forms is not advisable, since this oversimplification ignores important paleobiogeographic and evolutionary differences. The evolution of modern red deer was greatly influenced by 100 ky Milankovich cycles that shaped its ecological flexibility and intraspecific polymorphism (Ludt et al. 2004; Sommer et al. 2008; Meiri et al. 2013, 2017). The red deer is a new type of Pleistocene species, a typical representative of the Palearctic fauna with a vast area of distribution ranging from the

Tarim Area to Western Europe (Geist 1998). The arrival of *C. elaphus acoronatus* in Western Eurasia coincided with the extinction of both *Rucervus* and *Eucladoceros* and marked the end of the Villafranchian epoch.

Metacervocerus rhenanus ssp

This smaller cervid from VGr was mentioned by Radulescu et al. (2003) as in the '*Cervus* ex. *rhenanus/philisi* group', thus stressing its unresolved systematic affinity. The scanty and incomplete material that we have at our disposal does not allow us to make a definite conclusion on the taxonomic importance of some of the morphological peculiarities of this cervid; therefore, we report it as an undefined (possibly new) subspecies of *Metacervocerus rhenanus* that requires further study. The size of the *Metacervocerus* remains from Valea Grăunceanului (ca. 85 kg) corresponds to the largest specimens from Sènèze, and generally the Romanian form was ca. 30% heavier than *M. rhenanus* from Western Europe (ca. 60 kg). There are several species names attributed to a small-sized deer with three-pointed antlers (*Cervus rhenanus* Dubois, 1904; *C. philisi* Schaub, 1941; *C. perolensis* Azzaroli, 1952) that, according to De Vos et al. (1995), are synonymous. Heintz (1970) recognised two chronosubspecies of this deer in France: the larger *Metacervocerus rhenanus philisi* (Schaub, 1941) from Sènèze (= *C. philisi philisi* Schaub, 1941 according to Heintz 1970) and the smaller and older *M. rhenanus valliensis* (Heintz, 1970) from Saint-Vallier (= *C. philisi valliensis* Heintz, 1970).

Metacervocerus from the Olteţ River Valley is certainly closely related to *M. rhenanus* from Western Europe but is distinguished by a larger body size approaching that of *M. shansius* from Eastern Asia and *M. punjabiensis* from the Upper Siwaliks. *Metacervocerus* from Romania is more advanced than *M. shansius* in the stronger divergence of its pedicles. The distinction between *Metacervocerus* from the Olteţ River Valley and *M. punjabiensis* is even greater since the Siwalik species maintains such important primitive features as a relatively long braincase (Croitor and Robinson 2020). The Oltenian deer seems to be very similar to '*Cervus (Rusa) philisi*' from Liventsovka (Titov 2008) and '*Cervus (Rusa)*' sp. from Palantokan (Aleksperova 1964). According to Bukhsianidze and Koiava (2018), the fauna of Palantokan is coeval with Dmanisi or slightly older.

According to Titov (2008), unlike its western counterparts *Metacervocerus* from Liventsovka inhabited more arid and open landscapes. *Metacervocerus* from VGr and Liventsovka maintain a rather primitive type of dental morphology with a simple P₄ and a relatively long shearing premolar series. Therefore, the large form of *Metacervocerus* did not evolve particular morphological adaptations to more coarse forage and remained a typical opportunistic browser/mixed feeder. Nonetheless, the 30% body size increase itself represents a physiological adaptation to having a higher percentage of cellulose fibre in their diet (Janis 1976). Therefore, the ecological niche occupied by the large *Metacervocerus* from south-eastern Europe was rather different from that of western *M. rhenanus*. The smaller western European forms of *M. rhenanus* were more stenobiont than *Metacervocerus* from southeastern Europe and Transcaucasia and were more strongly tied to the forested biomes of Western Europe. It is interesting to note that smaller *M. rhenanus* remained locked in Western Europe and did not disperse into the Italian Peninsula that has yielded very diverse remains of small-sized cervids. The area of distribution of the larger form of *M. rhenanus* ssp. ranged from southern Romania to Azerbaijan; however, its biogeographic origin is linked to Eastern Asia, where the closely related *M. shansius* is known.

M. rhenanus from VGr is similar in size to *Axis ubensis* Vislobokova, 1988 from the Early Pleistocene of Navrukho

(Tajikistan), but in this case we are certainly dealing with two different species. *A. ubensis* is characterised by the primitive condition of relatively long and very little divergent pedicles, the first ramification of its antlers being situated lower and its antler beam strongly bowed backwards (Vislobokova 1988).

Dama eurygonos

In previous work (Terhune et al. 2020), we preliminarily reported the remains of a smaller cervid as a large form of *Croizetoceros*, stressing, however, that its systematic affinities remain unclear. Based on data collected on *Dama eurygonos* from the Upper Valdarno (Italy) in the comparative study, we now argue that this material has a greater affinity with the Early Pleistocene fallow deer. Sirakov et al. (2010) reported the presence of *Croizetoceros ramosus* from layers 11b-13 of Kozarnika (northwestern Bulgaria), but this material still awaits a detailed description and comparative analysis.

The early evolutionary stages of *Dama* are unknown. The remains of fallow deer from VGr represent the earliest well-dated finds of this cervid lineage. This is an endemic genus that appeared during the Early Pleistocene and dispersed across western and southern Europe and the Near East. The origin of *Dama* possibly can be traced to Pliocene *Metacervocerus* that was distinguished by its relatively short pedicles, one of the characteristic features of *Dama* (Croitor and Robinson 2020). *Dama* is characterised by highly specialised cranial and dental features, such as a strongly flexed braincase, short vertical pedicles, the loss of upper canines and a molarized fourth premolar (Croitor 2006a). The relatively long metapodials with deep and narrow epiphyses and less accentuated adaptations in their postcranial morphology for saltatorial locomotion argue for *D. eurygonos* as a rather cursorial cervid form (Croitor 2001, 2006a). The advanced molarisation of P⁴ in combination with the relatively broad and robust praemaxillary bones of the endemic small form of fallow deer from Pirro Nord (Italy) suggest an adaptation to coarse and fibrous Mediterranean vegetation (Croitor 2001). The four-tined antlers of Early Pleistocene fallow deer evolved through the adding of a crown tine on the posterior side of the main beam. This is the smallest ruminant species from Valea Grăunceanului with an estimated body mass ca. 60 kg. The geographic distribution of *Dama* in the Early Pleistocene suggests that this cervid lineage could not tolerate a continental climate with cold seasons. One can assume that ancient fallow deer were warm-loving cervids adapted to rather dry semi-open paleoecosystems of the Mediterranean type. Remains of the Early Pleistocene fallow deer *D. eurygonos* are abundant in Italy (Azzaroli 1992) but also are reported from the Lower Prut River Valley in Moldova (Croitor 2006a).

Mitilanotherium inexpectatum

While it was originally grouped with the giraffines (Samson and Rădulescu 1966), the genus *Mitilanotherium* is now considered a palaeotragine (Sickenberg 1967; Kostopoulos and Athanassiou 2005; Lyras and van der Geer 2007; Solounias 2007; Garrido and Arribas 2008; Garrido 2008b; 2011; Athanassiou 2014), being most similar in cranio-dental size and morphology to larger *Palaeotragus* species (Athanassiou 2014). Giraffid specimens previously referred to *Macedonitherium*, *Sogdianotherium* and *Palaeotragus priasovicus* are now placed in *Mitilanotherium* by most authors (Kostopoulos et al. 1996; Arribas et al. 2001; De Vos et al. 2002; Kostopoulos and Athanassiou 2005; Lyras and van der Geer 2007; Garrido and Arribas 2008; 2011; Athanassiou 2014; Iliopoulos and Roussiakis 2022; but see Vislobokova 2008).

The species *Mitilanotherium inexpectatum* has also been tentatively identified at Fonelas and Huélago in Spain, multiple sites in

Greece and Turkey and Dmanisi (De Vos et al. 2002; 2011; Athanassiou 2014; Iliopoulos and Roussiakis 2022). In addition to the type species, some researchers have, at least provisionally, recognised two other species of *Mitilanothereium*, *M. kuruksaense* and *M. martinii* (Sickenberg 1967; Sharapov 1974; Kostopoulos and Athanassiou 2005; Kahlke et al. 2011), although most recent studies group all *Mitilanothereium* specimens into a single species (De Vos et al. 2002; Lyras and van der Geer 2007; 2011; Athanassiou 2014) with size and shape differences among the putative species seen as relatively minor (2011). For example, the recently described cranium from Sésklo (see below) demonstrated that the dentition attributed to *M. kuruksaense* was not especially large compared to that of other *Mitilanothereium* specimens as some had previously stated (Kostopoulos and Athanassiou 2005; Garrido 2008b). Garrido and Arribas (2008) suggested that the specimens from Spain may represent a different species due to their greater size and gracility, but felt the material was too incomplete to assign it to a taxon.

Athanassiou (2014) recently described a nearly complete skull from the Early Pleistocene site of Sésklo that he noted was quite similar morphologically and metrically to the skull from Kuruksay attributed to *Mitilanothereium kuruksaense* by some authors. He also cited similarities between the cranial morphology of these two specimens and specimens attributed to the genus *Palaeotragus*, including a broad and dorsally flat skull that is elongated in the postorbital region and simple, pointed, laterally positioned ossicones located just over the orbits. Due to these similarities, Athanassiou (2014) argues for synonymising *Mitilanothereium* and *Palaeotragus* (as have, he notes, nearly all Russian researchers), with the latter genus taking priority, stating that ‘there are no sufficient differences to justify a taxonomic distinction at the genus level’ (p. 2). This synonymy had previously been argued for by Geraads (1986a) based on similarities between these genera in the location and morphology of the ossicones. This taxonomic revision has already been accepted by some researchers (e.g. Konidaris et al. 2015; Crégut-Bonnoure and Tsoukala 2017; Iliopoulos and Roussiakis 2022).

While it is clear that *Mitilanothereium* is more similar to *Palaeotragus* than to other palaeotragines (Sickenberg 1967; Garrido 2008b; Athanassiou 2014), there are potential reasons to be cautious about synonymising the two genera without a more extensive review of the evidence from both the cranial and postcranial skeleton. *Mitilanothereium* specimens typically have smaller maxillary premolar to molar tooth row ratios than *Palaeotragus* specimens (Athanassiou 2014), although differences are not as striking if one does not include the data for the Kuruksay specimen for which the premolar tooth row length is likely to be an underestimate based on the size of its P⁴ (Sharapov 1974; Athanassiou 2014). A relatively enlarged premolar row has been used as a diagnostic character for the genus *Palaeotragus* (Geraads 1978; Laskos and Kostopoulos 2022) so it is worth exploring whether this is a significant difference between the taxa. Specimens of *Mitilanothereium* also differ from most *Palaeotragus* in their rostrally oriented ossicones, with the only known *Palaeotragus* specimen having this morphology described as potentially abnormal (Bohlin 1926), and more protruding parietal crests (Sickenberg 1967; Athanassiou 2014). The Kuruksay specimen is said to differ from *Palaeotragus* in having a more elongated facial skeleton and straight nasals (Sharapov 1974). It is unclear if this is a consistent difference between the taxa given that the rostral-most aspect of the Sésklo specimen is missing (Athanassiou 2014). Finally, as noted above, the estimated length of the lower M3 of the type specimen is greater relative to its breadth than *Palalaeotragus* specimens of similar size.

In addition, as noted in description of the Volakas specimens (Sickenberg 1967) while the cranium of *Mitilanothereium* is quite similar to *Palaeotragus*, there are a number of differences between the genera in the size and morphology of the postcranial elements. For example, the metapodials of *Mitilanothereium* are similar in length but more robust than those of *P. rouenii*, but are longer while having reduced or similar robustity compared to those of larger *Palaeotragus* species (Athanassiou 2014; Rios et al. 2016; Laskos and Kostopoulos 2022; Table 19). Given that *Mitilanothereium* is a late surviving palaeotragine, this is inconsistent with the hypothesised evolutionary trend in *Palaeotragus* taxa of a reduction in limb length and increase in metapodial robusticity through time suggested by Laskos and Kostopoulos 2022. The estimated robusticity index, which has been used to taxonomically differentiate giraffids (Rios et al. 2016), for *Mitilanothereium* metapodial specimens is greater than that of *Palaeotragus rouenii* and the tentatively identified *P. berislavicus* specimens from Nikiti specimens (Kostopoulos et al. 1996; Kostopoulos 2009; Rios et al. 2016; Table 19), but less than that of *Palaeotragus coelophrys* (Athanassiou 2014). They would be categorised as ‘slender’ like *Okapia* (Sickenberg 1967; Rios et al. 2016). Data from the only relatively complete radius of *Mitilanothereium*, from Dafnero (Kostopoulos and Athanassiou 2005), are consistent with the metapodial data, with the Dafnero radius being elongated compared to specimens of *P. rouenii* and ‘large morph’ *Palaeotragus* species (*P. coelophrys* and *P. berislavicus*) but intermediate between the two in the size of its articular surfaces and its robusticity (Erdbrink 1978; Kostopoulos et al. 1996; De Vos et al. 2002; Kostopoulos and Athanassiou 2005; Kostopoulos 2009; Laskos and Kostopoulos 2022). While it is only one specimen, the only known relatively complete tibia of *Mitilanothereium* from Dafnero is unusually short, given the elongated *Mitilanothereium* metapodials and radii, and has a narrow distal articular surface relative to its antero-posterior length when compared to *Palaeotragus* species. The length and distal articular surface measurements for *Mitilanothereium* tibiae are more similar to the smaller *P. rouenii* than to ‘large morph’ *Palaeotragus* specimens (Kostopoulos et al. 1996; Kostopoulos and Athanassiou 2005; Kostopoulos 2009; Kostopoulos and Sen 2016; Laskos and Kostopoulos 2022; Table 19). *Mitilanothereium* was diagnosed as having reduced asymmetry between the lateral and medial proximal ridges of the astragalus trochlea (Samson and Rădulescu 1966) and the one specimen for which these measurements are available (VGr.0967) is distinct in this ratio from *Palaeotragus* (Erdbrink 1978; Kostopoulos 2009; Kostopoulos and Saraç 2005; Kostopoulos and Sen 2016; Solounias et al. 2016; Laskos and Kostopoulos 2022; Table 19). While these differences could very well be species-level rather than genus-level, we contend that it is best to maintain *Mitilanothereium* as a separate genus pending broader taxonomic and phylogenetic analyses, particularly since if *Mitilanothereium* and *Palaeotragus* are synonymised this would imply that the genus persisted for at least nine million years in Eurasia (Athanassiou 2014).

In the late Miocene giraffids are relatively common in Southern Eurasia with multiple genera of giraffids present (Solounias 2007; Athanassiou 2014; Iliopoulos and Roussiakis 2022), *Palaeotragus* being the most common of them (Laskos and Kostopoulos 2022). However, there appears to have been a dramatic loss of diversity after the Miocene such that in the Plio-Pleistocene only one genus, *Mitilanothereium*, possibly represented by only a single species, is documented in Europe (Athanassiou 2014), although recently an incomplete giraffid metatarsal was described from the site of Gephyra in Macedonia that is distinct in its dimensions, being shorter and more robust, and morphology, in lacking a deep furrow on its posterior surface, from *Mitilanothereium* specimens and, thus,

it may represent a different taxon (Crégut-Bonnoure and Tsoukala 2017). In addition, some have argued that there is a late surviving *Palaeotragus* species, *P. priasovicus*, from the Early Pleistocene sites of Liventsovka and Mukhai II (Godina and Baygusheva 1986; Amirkhanov et al. 2016), located just north of the Greater Caucasus mountains. However, while a mandible from Liventsovka lacks the diagnostic elongated M_3 of *M. inexpectatum* (Godina and Baygusheva 1985), *P. priasovicus* cranial specimens are morphologically and metrically quite similar, including in their ossicone orientation and morphology, to the skull from Sesklo (Athanassiou 2014) and the postcranial material attributed to this taxon is consistent in size and morphology with *Mitilanotherium* specimens.

Mitilanotherium is known primarily from sites dated to the Early Pleistocene in Western and Central Asia and Eastern Europe (e.g. Samson and Rădulescu 1966; Sickenberg 1967; Sharapov 1974; De Vos et al. 2002; Kostopoulos and Athanassiou 2005; Lyras and van der Geer 2007; Kahlke et al. 2011; Athanassiou 2014; Konidaris et al. 2015; Iliopoulos and Roussiakis 2022). While some have argued that the giraffid material from Dmanisi should be attributed to *Palaeotragus rouenii* (Vekua et al. 2008), measurements of the dental elements and metapodial proximal articular surfaces are more similar to *Mitilanotherium* specimens than to *P. rouenii* specimens (Vekua et al. 2008; Athanassiou 2014; Rios et al. 2016; Table 19). There are specimens attributed to this genus from two sites in Spain as well (Arribas et al. 2001; Garrido and Arribas 2008; Garrido 2008b, 2009; 2011), but interestingly not from French, German or Italian sites, which have a number of well documented Plio-Pleistocene faunal assemblages. There may be a large morph palaeotragine that is closely related to, or is congeneric with, *Mitilanotherium* from the Early Pleistocene of North Africa and the Middle East (Geraads 2010; Harris et al. 2010; Geraads et al. 2013). Some have suggested that the giraffids in Spain might be a descendant of this North African giraffid (Kostopoulos and Athanassiou 2005), but given the morphological similarities to Eastern European *Mitilanotherium* specimens it is more likely that the Spanish giraffids evolved from a group that dispersed from Eastern Europe during a brief period where climatic conditions made such a dispersal possible and that the lack of a fossil record in Central Europe is due to low population densities and sub-optimal environmental conditions for giraffids (2011; Palombo 2018). When present, *Mitilanotherium* makes up a very small percentage of the faunal assemblage (De Vos et al. 2002; Garrido 2008b) so it is also possible that its temporal and geographic range was more extensive than currently documented and that it was present in both Western and Central Europe during the Early Pleistocene (2011).

The earliest site from which *Mitilanotherium* has been clearly identified is Gülyazi in Turkey, which is dated to approximately 2.5 Ma, while the material from Libákos tentatively assigned to MNQ 19, approximately 1.2 Ma, currently represents the most recent date for the genus (Steensma 1988; 2011; van der Made 2013; Athanassiou 2014), although recent redating of Libákos to 1.5–2.0 Ma (Koufos and Tamvakis 2022) would suggest a more restricted temporal range, which might mean that the type specimen is the most recent currently recognised *Mitilanotherium*. The temporal range of *Mitilanotherium* may extend back to MN15 with the taxon evolving locally from a *Palaeotragus* species, but the evidence is equivocal at best, due to the paucity of well-preserved faunal assemblages from this time period in Western Asia and Europe (Athanassiou 2014). Another possibility is that palaeotragines were extirpated in Western Asia and Eastern Europe at the end of the Miocene and *Mitilanotherium* is the descendant of a migrant from further east in Asia (Sickenberg 1967; Godina and

Baygusheva 1986; Vislobokova 2008; Arribas et al. 2009; Athanassiou 2014).

Mitilanotherium is mostly found in environments that have been reconstructed as dry and open, where its primary niche was likely that of a browsing taxon given its brachyodont dentition and high occlusal relief, feeding in the patchy shrubs and woodland in these areas (Sharapov 1974; 2011; Athanassiou 2014). It has been described as a ‘specialized open-landscape species’ (Croitor 2018a, p. 283) and its presence has been used by some to argue for the presence of savanna-like or dry and open landscapes at a site (De Vos et al. 2002; Boulbes et al. 2014), although others have argued that it is indicative of bushy or woody environments (Kahlke et al. 2011).

Post-Pachycrocuta event ruminants

Megalovis latifrons

Even after Schaub in 1923 created the new genus and species *Megalovis latifrons* based on cranial material from Senezé, the systematic position of this wildebeest-sized bovid remained unclear for a long time. Sokolov (1953) regarded *M. latifrons* as a Caprinae *incertae sedis*. Guérin (1965) placed *Megalovis* in Rupicaprinae as an *incertae sedis* genus together with the informal groups of *Rupicapra*, *Nemorhaedus* with *Caproicornis* and *Budorcas*. Duvernois and Guérin (1989) placed *M. latifrons* in an arbitrary group of antelopes. Partly, the unclear systematic position of *Megalovis* was due to the fact that the type specimen of *M. latifrons* (Schaub 1943), (Figures 5–6) most probably belongs to a female (Crégut-Bonnoure and Dmitrijevic 2006), a fact that made the systematic interpretations of its cranial and horn core morphology difficult. Finally, Gentry (1970) and Gentry and Gentry (1978) recognised the relationship of *Megalovis* with modern Ovibovini. This viewpoint is accepted by Crégut-Bonnoure (2007), who also placed *Megalovis* in the tribe Ovibovini together with *Soergelia*, *Praeovibos* and *Ovibos*.

The finding of *Megalovis* remains in the Balkans area is not uncommon. According to Crégut-Bonnoure (2007), *M. latifrons* from Romania could belong to a new subspecies. However, the fossil material from Senezé, the type locality of *M. latifrons*, and from Fântâna lui Mitilan is quite restricted; therefore, we refrain from comments on the subspecies subdivision of *M. latifrons*. Crégut-Bonnoure and Dmitrijevic (2006) described a new species *Megalovis balcanicus* based on a partial male skull from the late Early Pleistocene of Trlica (MNQ20). *M. balcanicus* is distinguished from the typical Senezé form by the shape of its horn cores, features of the frontoparietal area correlated with horn core shape and some minor details of its dental morphology (Crégut-Bonnoure and Dmitrijevic 2006). According to Crégut-Bonnoure (2007), this species could also be present in layers 12 and 11c of Kozarnika. Since the type specimens of *M. latifrons* and *M. balcanicus* belong to a female and a male, respectively, the diagnostic distinctions based on the cranial material are unlikely to be reliable if one takes into account the sexual dimorphism that is characteristic of ovibovines. Individual variation of the molars of *Megalovis* has not been studied on sufficient amounts of material; therefore, the systematic importance of the minor variants of the dental morphology indicated by Crégut-Bonnoure and Dmitrijevic (2006) is not clear. Thus, one cannot exclude the possibility that *M. balcanicus* is a junior synonym of *M. latifrons*.

It is very probable that the skeletal remains of *M. latifrons* from FM belong to one male individual. If this is the case, the length ratios of the anterior limb bones reveal some peculiar ecomorphological characteristics of this species. The metacarpal of *M. latifrons*

from FM is particularly short when compared to the length of the radius (66.2%) and *M. latifrons* approaches *Capra caucasica* and *C. aegagrus* reported by Egorov (1955) in this feature as the most short-limbed mountain climbers. A relatively long radius in bovids also represents a specific feature of mountain adapted bovids (Egorov 1955; Gambarian 1972; Köhler 1993). It is important to mention that *M. latifrons* maintains limb proportions similar to those of the specialised mountain rupicaprine bovid *Gallogoral meneghini* from S n ze (Gu rin 1965). Nonetheless, *M. latifrons* is unlikely to be a good mountain climber because of its large body size (ca. 300–350 kg according to measurements of its craniodental variables, adapted from Schaub 1943). Generally, body mass in mountain ruminants is a relatively conservative ecomorphological feature that varies very little during the evolutionary development of a lineage and remains stable even under conditions of climate change (Brugal and Croitor 2007). This remarkable stability of body mass in mountain bovids is most probably conditioned by stabilising selection towards an optimal body size imposed by mountain habitats (Croitor 2016c). The body mass of the largest modern mountain-adapted bovids does not exceed 150 kg (Sokolov 1959). The estimated body mass of *Gallogoral meneghini* (ca. 160 kg) is close to this maximum threshold. The origin of such an unusual combination of anatomical and ecomorphological characters in *Megalovis* should be sought in the evolutionary history of this genus. Bibi et al. (2009) related the dispersal of *Makapania* – the Early Pleistocene ovibovine genus closely related to *Megalovis* – into the African continent with the beginning of the Early Pleistocene glacial cycles and general climate cooling. This observation is interesting, since it explains the early evolutionary history of the *Megalovis-Makapania* lineage. As in the case of *Pliotragus*, the early evolutionary stages of *Megalovis-Makapania* are associated with mountain habitats with relatively low temperatures. This resistance to low temperatures enabled Early Pleistocene ovibovines to disperse into lowlands during the cold phases of the Early Pleistocene glacial cycles. Unlike *Pliotragus*, *Megalovis* achieved a more advanced evolutionary specialisation to mountain habitats. Such a high degree of specialisation restricted the evolutionary potential of early ovibovines, which could not follow the evolutionary path of cursoriality as a predator avoidance strategy. Therefore, evolution towards a body mass increase represented the only possibility for *Megalovis* as an anti-predator strategy. The cold-adapted lineage of early ovibovines was very successful during the Early Pleistocene and could adapt to a broad range of biogeographic zones: the distribution of *Megalovis* ranged along the Alpine-Himalayan Mountain belt from eastern Asia to Western Europe (R dulescu and Samson 1962), while *Makapania* dispersed as far as South Africa (Gentry 1970).

The general shape of the horn cores and limb bones of *Megalovis latifrons* correspond to K hler's (1993) "mountain rammer" ecological type of artiodactyl. Most probably, in this case we are dealing with another evolutionary "superimposition" of adaptations to different environments, as in *P. ardeus* and, for example, in the modern antelope *Saiga tatarica* that shows adaptations to open plains superimposed on mountain-habitat morphofunctional features (Sokolov 1964). The relatively short metacarpals in *Megalovis latifrons* may also be attributed to the negative correlation between relative metapodial length and body mass that is often observed in hoofed mammals (Gambarian 1972). The narrow and pointed premaxillary bones in the skull from S n ze (Schaub 1943), (Figure 5) represent another important ecological specialisation, which,

according to the ecomorphological study of Solounias and Moelleken (1993), suggest that *M. latifrons* was a selective browser. One can assume that *M. latifrons* could equally inhabit riparian forests, forested foothills and forested low mountains but was too large for high rocky mountains. Therefore, we assume that *M. latifrons* was better adapted to wooded plain and low mountain environments.

Eucladoceros-like deer

The systematic position of the *Eucladoceros*-like cervid from FM remains unclear. The scarce sample does not allow for an understanding of the nature of the main morphological peculiarity of this cervid form: the relatively short premolar series and unmolarized P₄ with a reduced posterior part of the crown. We cannot exclude the individual character of such a peculiar P₄ shape. The low profile of the middle-stage wear in the M₃ FM.0135 with practically unexpressed cusps may suggest a poor quality of the forage that is close to the limits of its ecological tolerance. An understanding of the systematic position of this poorly known cervid could be possible if/when new fossil material becomes available.

Fallow deer

The absence of antler material does not allow the establishment of the species the fallow deer from FM belongs to. Some diagnostic remains of fallow deer come from the south of the Balkan Peninsula. Athanassiou (2021) reported the presence of *Dama vallonnetensis* in the Early Pleistocene of Libakos (North Greece) that probably is close to the age of FM (Vislobokova and Agadjanian 2016). The antler fragment with a part of a frontal bone from Megalopolis (Greece) described by Sickenberg (1975): pl. IX [IV], (Figure 1) as *Cervus* sp. certainly belongs to a fallow deer. *D. vallonnetensis* is present in the faunas of Capena (Italy), Vallonnet (France), Untermassfeld (Central Germany) and Gruta da Aroeira (Portugal) (Kahlke 1997; Croitor 2006a; Croitor et al. 2019). The loss of the middle tine is the most interesting evolutionary feature of *D. vallonnetensis* that distinguishes this species from *D. eurygonos*. The ecomorphological significance of such antler simplification is not clear yet. The simplified antlers of *D. eurygonos* are reminiscent of the antlers of tropical and subtropical cervids, such as *Rucervus duvaucelii* and *Panolia eldii* that, unlike Palearctic cervids, do not possess the middle (trez) tine. One can assume that the antler simplification in fallow deer could evolve in warm climate conditions with mild winter seasons. The mesowear and microwear analyses of the quite limited dental material from F nt na lui Mitil n provided the expected result for a cervid of such small size; a browsing diet with a switch to grazing during the dry winter season (Curran et al. 2021). According to Kahlke (2006), *D. vallonnetensis* from Untermassfeld inhabited open parklands outside river valleys like modern fallow deer. A generally temperate and warm climate free from extreme seasonal temperature fluctuations in Untermassfeld is confirmed by the presence of several typically Mediterranean species and *Hippopotamus amphibius* (Kahlke 2006). In Gruta da Aroeira (Portugal), *D. vallonnetensis* is associated with fossil remains and the hunting activity of archaic *Homo* (Croitor et al. 2019). The small vertebrate assemblage from Gruta da Aroeira points to an open-woodland landscape under relatively mild and humid climate conditions (Lopez-Garc a et al. 2018).

Praemegaceros obscurus

The species *Cervus obscurus* was established by Abbazzi et al. 1999 on the basis of a series of antler fragments and frontal bones from the Forest Bed Formation near Mundesley. Later, similar cervid forms were described from the Early Pleistocene of Romania and

Italy as *Allocaenelaphus arambourgi* Rădulescu and Samson, 1967 and *Megacerooides boldrinii* Azzaroli and Mazza, 1992 correspondingly. Currently, those two species names are regarded as junior synonyms of *Praemegaceros obscurus* (Croitor 2006b). The strong basal tine situated very close to the burr and the caudally directed straight beam with irregular cross-section represent the main diagnostic features that distinguish *P. obscurus* from another closely related Early Pleistocene species, *Praemegaceros pliotarandoides*. The differences in antler crown bauplan in *Praemegaceros* indicate the presence of two independent lineages characterised by the dichotomous pattern of the distal crown (*P. pliotarandoides* and *P. verticornis*) (see Sickenberg 1975) and the crown formed by distal tines inserted on the anterior side of the beam (*P. obscurus* and *P. dawkinsi*) (Azzaroli and Mazza 1992; Croitor 2006b). Croitor (2006b) proposed to give to those two groups of *Praemegaceros* the taxonomic status of subgenera *P. (Praemegaceros)* for the type species *P. dawkinsi* and *P. (Orthogonoceros)* for the type species *P. verticornis*. Both lineages appear in southeastern Europe in the Early Pleistocene but show some differences in geographic distribution and different degrees of antler evolutionary specialisation. The subgenus *Orthogonoceros* is more advanced in an almost complete reduction of the basal tine, which is present in *P. pliotarandoides* as a small vestige. *P. pliotarandoides* may have originated from *Praemegaceros* sp. reported by Vislobokova (1988) from Lakhuti-2, Tajikistan.

P. obscurus is the only *Praemegaceros* species recorded in the southern part of Eurasia. Those findings are important, since they come from classic palaeoanthropological sites of Dmanisi in the Transcaucasian region (Vekua, Bendukidze, Kiladze 2010) and Ubeidya in the Near East (Croitor 2006b). The strong basal tine in *P. obscurus* situated very close to the burr and the strong backward direction of the beam with an irregular cross-section suggest the close relationship of *P. obscurus* with *Panolia eldii*; thus, a South-Asian origin of this large-sized deer may be assumed (Croitor 2018a). Strong basal and dorsal tines function as eye protection during combat suggesting that the antlers in *P. obscurus* served as an effective weapon rather than a visual signal. Nonetheless, the presence of a middle tine in the antlers of *P. obscurus* from Dmanisi (Vekua, Bendukidze, Kiladze 2010) (Figure 7) suggests that we are dealing with a typical Palearctic species. A mesowear analysis of a rather small sample from the Late Villafranchian site of Ceysaguet (France) defines *P. obscurus* as an attrition dominated mixed feeder inhabiting grasslands with wooded habitats (Kaiser and Croitor 2004).

The ecological group of 'giant deer' is characterised by a gradual adaptation to open landscapes and has no ecological analogies in modern faunas (Vislobokova 2012). The large body size in ruminant herbivores represents a well-known antipredator adaptation in open landscape (Geist 1998) and an important physiological adjustment that permits them to digest a larger number of vegetal fibres in forage (Janis 1976). *P. obscurus*, with a body mass that attained ca. 400 kg, was one of the largest cervid species in the Dacian Basin Area.

The oldest remains of *P. obscurus* from the Dacian Basin and the entire European continent come from the Early Pleistocene of Izvoru-1 (Rădulescu and Samson 1986). According to Rădulescu and Samson (1986), the deposits of Izvoru-1 correspond to the early Eburonian and the middle part of 'Sénèze zone'. Therefore, the occurrences of *P. obscurus* in Georgia and the Dacian Basin were almost simultaneous. The dispersal of *P. obscurus* into the Italian Peninsula took place somewhat later, ca. 1.4 Ma (Gliozzi et al. 1997). The area of distribution of *P. obscurus* ranged from Ubeidya and Dmanisi in southwestern Asia, Salcia in Southeastern Europe to the Forest Bed Formation in northwestern

Europe. The only securely dated record of typical *P. obscurus* in Western Europe comes from the last stage of the Late Villafranchian of Ceysaguet (France), ca. 1.2 Ma (Croitor and Bonifay 2001) suggesting a rather late persistence of this species in Western Europe.

Praemegaceros cf. *mosbachensis*

A particular form of *Praemegaceros* from the upper levels of FM apparently represents a more advanced local form that follows the evolutionary specialisation of antlers already described in *Praemegaceros mosbachensis* (Soergel 1926) from the lower level of Mosbach, Germany. *P. mosbachensis* attained the body size of *P. verticornis* but was distinguished by the presence of a rather strong basal tine situated very close to the burr (Soergel 1927). The development of a basal tine and the straight proximal portion of the antler being sloped backward from the burr in *P. mosbachensis* approaches the morphology of *P. obscurus*; however, the former species shows a set of more advanced features, such as reduction of the size of the basal tine, shortening of the antler segment between the dorsal (second) tine and the burr and strong flattening of the beam above the middle tine. Kahlke (1956) regarded *P. mosbachensis* as a variant of *P. verticornis*, thus accepting a very broad range of individual variation of antlers in this species. According to Rădulescu and Samson (1967), *P. mosbachensis* represents a transitional evolutionary link between *P. obscurus* (*Allocaenelaphus arambourgi* according to the cited authors) and *P. dawkinsi*, an endemic specialised form from the Middle Pleistocene of the Forest Bed Formation (England). Generally, *P. mosbachensis* follows the evolutionary trend described by Sickenberg (1975) for the *P. pliotarandoides* – *P. verticornis* lineage and attains the level of evolutionary specialisation of *P. (Orthogonoceros) verticornis*, representing a good example of evolutionary parallelism (Soergel 1927). *Praemegaceros* from the upper levels of Fântâna lui Mitilan has specialisations in antler shape similar to *P. mosbachensis*; however, it is as small as *Eucladoceros* and possibly resulted from a local evolutionary event. Unlike *P. dawkinsi*, the endemic western European descent of *P. mosbachensis*, *P. cf. mosbachensis* from the Dacian Basin maintains a well-developed dorsal tine; therefore, we are dealing with two parallel evolutionary processes that independently took place in northwestern Europe and in the Dacian Basin and adjacent areas.

The evolutionary specialisation of *P. cf. mosbachensis* from the Dacian Basin was very fast and took place between the *Pachyrocota* event and the End-Villafranchian event. A similar small *Praemegaceros* with a vestigial basal tine is found at Chițcani (the Republic of Moldova). The Jaramillo palaeomagnetic event (0.98–1.07 mln. years) is recorded in the upper alluvium of the VII terrace of the stratotype section of Chițcani (Chepalyga et al. 2012), thus suggesting an age of the final Villafranchian stage for *P. cf. mosbachensis* from this site.

Early Pleistocene ruminants of the Dacian Basin and the Pachyrocota event

The assemblage of ruminants from VGr from the Dacian Basin is characterised by a set of features that reveals a particular paleobiogeographic character of the region. The fauna of VGr is dominated by Pliocene faunal holdovers, such as *Mitilanotherium inexpectatum*, *Rucervus radulescui*, *Pliotragus ardeus* and *Gazellospira torticornis*. Two of them (*R. radulescui* and *P. ardeus*) are dominant species in the ruminant assemblage. Each of these Pliocene relic species are characterised by evolutionary adaptations to sparsely wooded, dry and warm plains (Curran et al. 2021), superimposed on rather diverse initial evolutionary specialisations, such as the

mountain habitat specialisation in *P. ardeus* and adaptations to forest habitats in *G. torticornis*. The seasonal drop of temperatures seems to be the main limiting factor of the relic ruminants from VGr. This assumption is confirmed by the fact that *Mitilanotherium* likely had a disrupted area of distribution in Western Eurasia, surviving in the refugia of the Iberian Peninsula and the Balkans. The Pliocene lineage of barasingha-like deer *R. (Arvernoceros) ardei* also survived into the Pleistocene in the glacial refugia of the Iberian Peninsula where it evolved into endemic *Haploidoceros mediterraneus* (Croitor et al. 2020) and in the Dacian Basin where it is represented by *R. (Arvernoceros) radulescui* (Croitor 2018a).

Another group of pre-*Pachycrocuta* Oltanian ruminant species have a clear East Asian paleobiogeographic origin: *Metacervocerus rhenanus* ssp., *Alces gallicus*, *Eucladoceros ctenoides*, *E. dicranios* and possibly *Bison (Eobison) sp.* *Bison (Eobison)* and *Metacervocerus* are East Asian faunal elements that also dispersed into the Indian subcontinent. The exact character of relationships between *Bison (Eobison) sivalensis* from the Indian Subcontinent and *B. (Eobison) sp.* from southeastern Europe remain unclear (Kostopoulos et al. 2018; Sorbelli et al. 2021); however, the large form of *M. rhenanus* shows a stronger affinity with *Metacervocerus shansius* from Shanxi (China) than with *M. punjabiensis* from the Siwaliks (Croitor and Robinson 2020).

Alces gallicus is a highly specialised telemetacarpal deer that arrived in Western Eurasia from East Asian temperate latitudes. Its particular adaptation to open river meadows enabled a vast continent-wide latitudinal dispersal. However, extremely dry climates, a lack of water sources and dense forests and mountains were unsurmountable biogeographic obstacles for this species. This explains the absence of *A. gallicus* in the Italian and Iberian peninsulas and in the southern part of the Balkans.

Eucladoceros is a Middle Villafranchian faunal element that by the Late Villafranchian evolved into two well-distinguished species: *E. dicranios* and *E. ctenoides*. *Eucladoceros ctenoides* was evolutionarily flexible and gave rise to several subspecies, including *E. ctenoides ctenoides* from the Italian Peninsula and *E. ctenoides falconeri* from Western Europe. The presence of a small number of remains of *E. ctenoides falconeri* in the VGr fauna reveals a biogeographic contact between the Dacian Basin and Western Europe. This biogeographic connection was likely possible due to the Early Pleistocene West Eurasian forest biome, since *E. ctenoides falconeri* shows the most advanced specialisations to forest habitats among *Eucladoceros*. The distribution of the lightly built bison-like *Leptobos etruscus* recorded in the Early Pleistocene of Leu also was related to the Western Eurasian forest biome (Croitor 2013). However, the biogeographic origin of *L. etruscus* was different. The oldest record of *L. etruscus* comes from Kotzahuri (Georgia) and its dispersal westwards is bound to warm foothill and mountain forests (Croitor and Popescu 2011).

The evolution of *E. dicranios* took place in southeastern Europe and the Dacian Basin served as a dispersal path for this species towards the Italian Peninsula and Western Europe. *Dama* is an endemic cervid genus of Western Eurasia that, like *E. dicranios*, evolved in warm and relatively dry environmental conditions similar to the modern Mediterranean biome.

Generally, the community of ruminants from VGr is dominated by medium-sized species (200–300 kg), such as *E. dicranios*, *E. ctenoides falconeri*, *R. radulescui*, *G. torticornis* and *P. ardeus*. It is interesting to note that all those species are ecologically rather opportunistic and could coexist in the same faunal assemblage only due to well-expressed ecological partitioning (Curran et al. 2021). The predominance of the medium-sized ruminants in pre-*Pachycrocuta* Dacian Basin fauna may be regarded as reminiscent of the diversified herbivore guilds of African savannas, but this

similarity is superficial, since African ‘Tertiary’ ecosystems attained a steady climax community stage with highly co-adapted species and well-adjusted ecological partitioning (Janis 1976). This is not the case in the community of opportunistic herbivores from VGr; therefore, the ecological partitioning among species with similar resource requirements most probably resulted from the choice of different biotopes. This explains the predominance of very few species in the fauna from VGr, which, apparently, were characteristic for the biotope represented by the mammal assemblage from VGr (Terhune et al. 2020).

The comparison of the assemblage of ruminants from VGr and La Pietriș with the roughly coeval layer 13 of Kozarnika reveals some difference in species composition that certainly represents local biotope peculiarities. The fauna from Kozarnika contains such mountain bovid genera as *Ovis*, *Hemitragus* and *Procamptoceras* (Sirakov et al., 2010), which are absent in the fauna from Valea Grăunceanului. Sirakov et al. (2010) also mention *Soergelia* sp. in the faunal assemblage composition from layer 13 of Kozarnika, but this statement requires confirmation. Another particular biotope-specific coeval ruminant community dominated by few bovid species (*Gazella bouvrainae*, *Gallogoral meneghinii* and *Gazellospira torticornis*) was recently reported from the Early Pleistocene of Karnezeika, Southern Greece (Sianis et al. 2022). This implies that assemblages of fossil ruminants are good indicators of local environments, and a certain range of diversity of local faunas in the same area should be expected.

The *Pachycrocuta* event in the Dacian Basin is marked by the extinction of the Pliocene holdovers (*Rucervus*, *Gazellospira* and *Pliotragus*) and the dispersal of the large-sized deer *Praemegaceros obscurus* that appears for the first time in Europe at Izvoru-1. *Mitilanotherium* is an exceptional case of a Pliocene survivor in the Dacian Basin after the *Pachycrocuta* faunal turnover. One can assume that the persistence of *Mitilanotherium* was partially driven by the specific ecological niche that allowed this giraffid, unlike other ruminants from the Dacian Basin, to avoid competition for resources with newcomers. The increase of woodland density reported for the biota from Fântâna lui Mitilan (Curran et al. 2021) would have been a favourable factor for *Mitilanotherium* enabling the species to overcome the *Pachycrocuta* faunal turnover in the Dacian Basin area.

Praemegaceros obscurus is a remarkable faunal element since it appears almost simultaneously in the Dacian Basin and Dmanisi and possibly has a south Asian origin related to *Panolia* sp. from the Siwaliks (Croitor 2018b). *P. obscurus* dispersed further towards the Italian Peninsula and northwest Europe but remains unknown in the middle latitude areas with a strong continental climate. Remains of *P. obscurus* from Ubeidya represent the only known instance of the presence of a large-sized deer in the Near East. In the Dacian Basin, *P. obscurus* was exposed to an evolutionary selection pressure that resulted in reduced body size and a reduction of the basal tine and the proximal portion of the antler beam, characteristics that one can see in *P. cf. mosbachensis* from Fântâna lui Mitilan. Possibly, some of cervid remains from Fântâna lui Mitilan described here as *Eucladoceros* sp. actually belong to *P. cf. mosbachensis*. It is important to note that the remains of *P. obscurus* from Ubeidya (= *Praemegaceros verticornis* fide Geraads 1986b) and Farneta (Italy) (= *Megaceroides boldrinii* Azzaroli and Mazza, 1992) maintained the initial antler morphology and do not show any trend towards a reduction of the proximal parts of the antlers.

Megalovis latifrons may be regarded as an East Asian faunal element characteristic of post-*Pachycrocuta* faunas of the Balkans and possibly of the rest of Europe, including Senezèze. Some representatives of the Early Pleistocene East Asian fauna that appeared in

Transcaucasia never reached the Dacian Basin. This is the case for *Sinomegaceros insolitus* (= *Arvernoceros insolitus* Vekua, Bendukidze, Kiladze 2010), a peculiar species of the Dmanisi fauna that seems to be closely related to *Sinomegaceros stavropolensis* (= *Megaloceros stavropolensis* Titov and Shvyreva 2016) from the Early Pleistocene of Ciscaucasia.

The fallow deer from Fântâna lui Mitilan is a Mediterranean faunal element that most likely is conspecific with *Dama vallonensis*. Nonetheless, the remains of fallow deer are still unknown from the Early Pleistocene of Anatolia and the Near East, although some isolated P₄s of small-sized deer from Ubeidiya show a high degree of molarization as in *Dama* (Geraads 1986b) pl. II, (Figure 7).

A hierarchical cluster analysis revealed specific paleobiogeographic contexts of the Early Pleistocene faunas from the Dacian Basin shortly before and after the *Pachycrocuta* faunal event (Figure 32). Before the *Pachycrocuta* event, the Dacian Basin biogeographically is associated with Central Asia (we mostly consider the fauna from Kuruksai from the Tajik Basin) and Southeastern Europe that can be termed the Eurasian continental open woodland. This biogeographic unity is characterised by the presence of the Pliocene faunal relics (such as Giraffidae, *Gazellospira* and *Rucervus*) and faunal elements of East Asian origin (*Alces* and *Metacervocerus*). Transcaucasia is associated with the South Balkans and Western Europe as those faunas show the ‘typical’ Villafranchian character (Azzaroli 1983; Azzaroli et al. 1986; Gliozzi et al. 1997; Crégut-Bonnoure 2007; Palombo et al. 2010; Martínez-Navarro et al. 2011; Koufos and Kostopoulos 2016; Bukhsianidze and Koiava 2018). This vast Transcaucasian-European biogeographic area is called here the Eurasian western

forest biome. It is important to note the detached position on the dendrogram of the faunas from Bethlehem and Gadera that, as noted by Hooijer (1958) in his characterisation of the fauna from Bethlehem, bear an ‘African stamp’ on their biogeographic affinity. Rabinovich and Lister (2017) consider that the fauna from Bethlehem could have an older Pliocene age according to the primitive morphology of the elephantid remains. Nonetheless, the difficulty of defining the age of the Bethlehem fauna (see Rabinovich and Lister 2017 and references therein) is a consequence of the stability of Levant ecosystems before the *Pachycrocuta* event.

The paleobiogeographic configuration in Western Eurasia after the *Pachycrocuta* event is different (Figure 32-B). The fauna from FM from the Dacian Basin is associated with faunas of Mediterranean Europe. In Western Europe, a humid climate refugium (*sensu* Croitor and Brugal 2007) is emerging. The community of ruminants from Ubeidiya associates the Levant Corridor with the Mediterranean biome of southern Europe and Western Europe. This biogeographic affinity is supported first of all by the presence of cervids in Ubeidiya, opportunistic and ecologically flexible ruminants (Geist 1998) that indicate a deep ecosystem restructuring in the Levant after the *Pachycrocuta* event. Eastern Europe and Central Asia remain biogeographically closely related, but the biogeographic dissimilarity between the Dacian Basin and Eastern Europe became very important. The results of pollen analysis from the Olteț River Valley revealed the insignificant presence of pollen of typically Palearctic trees and shrubs (*Pinus*, *Picea*, *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Tilia*, *Carpinus* and *Fagus*) that apparently are related to the mountain belt ecosystems of Western Eurasia (Curran et al. 2021). Those mountain broad-leaved and mixed

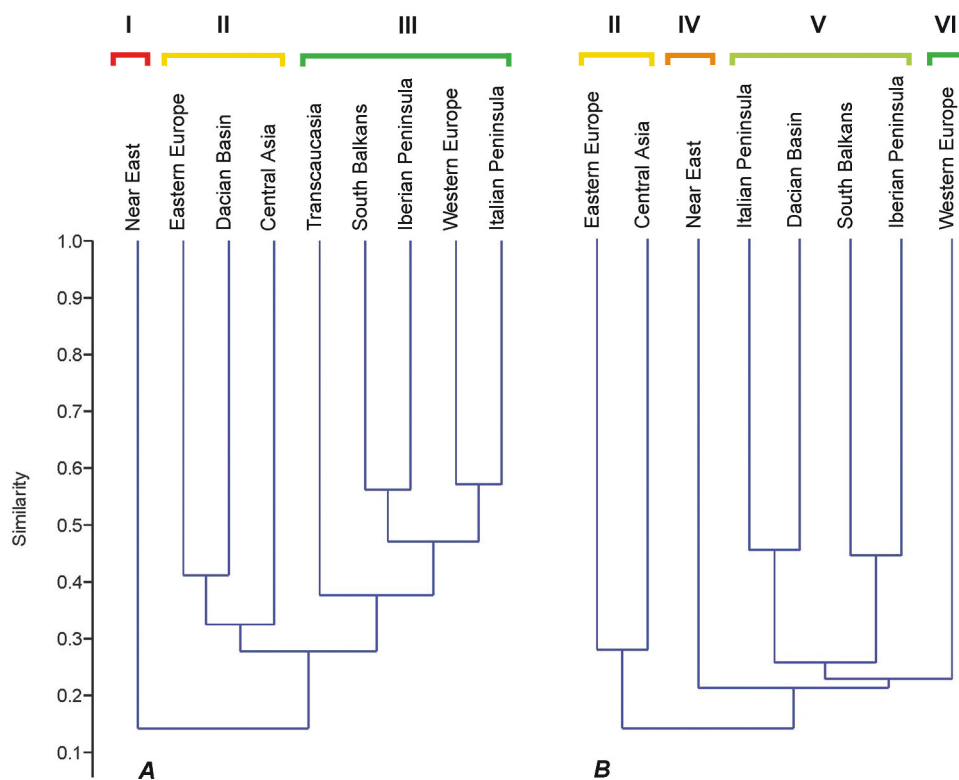


Figure 32. Paleobiogeographic zones before (A) and after *Pachycrocuta* event (B): I, Afrotropical savanna; II, Eurasian continental open woodland; III, Eurasian western forest biome; IV, Eastern Mediterranean savanna; V, Northern Mediterranean savanna; VI, Western humid forest refugium.

forests mark the boundary between the Mediterranean paleobiogeographic area and the inland Eurasian paleobiogeographic zone with continental dry climate and accentuated seasonality that is dominated by open planes and sparse woodlands (Vislobokova 2008; Croitor 2018b).

Implications to early hominin dispersals in Western Eurasia

Hominins are first documented in Western Eurasia at the site of Dmanisi, Georgia, dated to approximately 1.85 Ma (Lordkipanidze et al. 2007). Following that, the next well-documented site with clear evidence of hominins in Europe is Barranco León (Orce), Spain, at about 1.4 Ma (Toro-Moyano et al. 2013). While there are well-dated sites in East Asia documenting the presence of hominins relatively soon after they first left Africa (e.g. Ferring et al. 2011), the timing of hominin dispersals into Europe west of Dmanisi is not well understood. However, it is suggested to be most probable that hominins would have dispersed through Eastern Europe as they spread through the continent (O'Regan et al. 2011; Parés et al. 2013; Iovita et al. 2014).

Our analyses provide evidence for a stronger connection between the Dacian Basin and Southeastern Europe before the *Pachycrocuta* event (Figure 32), with a number of taxa documented above as being present at both Dmanisi and Valea Grăunceanului (e.g. *A. gallicus*, *M. inexpectatum* and *P. obscurus*). Others have also noted similarities between the fauna at Dmanisi and European Late Villafranchian sites (Tappen 2009). As for the Iberian Peninsula and Transcaucasia, the Dacian Basin acted as a refugium for temperature-sensitive savanna species during the Early Pleistocene. This is one of the most important paleobiogeographic features of the Dacian Basin that requires additional attention in the context of early hominin dispersals in Western Eurasia.

The dispersals of early hominins and other African species into Eurasia are often regarded as a rather intrinsic and sudden enlargement of species' area of distribution caused by new evolutionary, ecological and social acquisitions that were particularly suitable in the changing Early Pleistocene environments of southern Eurasia (Carbonell et al. 2008; Bartolini-Lucenti et al. 2022 and references therein). However, African-Eurasian faunal exchanges were also greatly influenced by larger-scale climate and geographic changes. Böhme et al. (2021) demonstrated that the arid and hyperarid climate alternations in Arabia played an important role in faunal exchange between Africa and Eurasia and caused the isolated endemic (at the continental scale) evolution of African taxa during the major part of the Late Neogene. In particular, the sustained hyperarid period between 5.6 and 3.3 Ma caused the biogeographic isolation of the Afrotropical realm (Böhme et al. 2021). According to the cited authors, the mid-Piacenzian warming and retreat of deserts enabled bi-directional faunal exchange between Africa and Eurasia that continued during the Pleistocene.

One can assume that the fauna of Bethlehem (>3–2.5 Ma; see the discussion in Rabinovich and Lister 2017) represents an early stage of biogeographic evolution after the deserts retreat and the extension of the Afrotropical zoogeographic realm into the Levant. This extension of the Afrotropical realm corresponds to an African-Eurasian faunal exchange; however, this should be regarded as an episodic shift of biogeographic borders between the Afrotropical and Palearctic realms. Further climate shifts caused the crash of Afrotropical ecosystems in the Levant and the retreat of the Afrotropical zoogeographic realm. Relic populations of some Afrotropical species, including hominins, could persist with varying degrees of success in biogeographic refugia of southwestern Asia. Possibly, the hominin presence in Dmanisi is such a case, contrary to the broadly accepted assumption that the Dmanisi faunal

assemblage represents evidence of a sort of biogeographic cross-road, where African species meet their Eurasian counterparts (Bartolini-Lucenti et al. 2022). The hypothesis proposed here of Dmanisi as a biogeographic refugium is supported by multiple lines of evidence that the Transcaucasian region, and the territory of modern Georgia in particular, acted as a refugium during different periods for warm-loving rodents, primates and cervids (Vekua, Bendukidze, Kiladze 2010; Croitor 2018a, b). The new interpretation of the paleobiogeographic record challenges the presumed role of the Levant as a perennial Palearctic region that acted as a biogeographic obstacle and selective filter for Afrotropical species dispersals (Rolland 1997). Louys and Turner (2012) discussed the importance of climate refugia for hominin persistence and dispersals in Southeast Asia; however, the refugial character of early hominin populations in southwestern Eurasia has never been considered. The Early Pleistocene refugia in southwestern Asia of Afrotropical species could act as footholds for further dispersals in Eurasia. This new stage of paleobiogeographic evolution could have been triggered by the *Pachycrocuta* event that marked the emergence of the Mediterranean biogeographic zone that comprised southeastern peninsulas closely associated with the Levant. The landbridge between Anatolia and the Balkan Peninsula existed during most of Early Pleistocene enabling the faunal exchange between the Near East and southeastern Europe (Krijgsman et al. 2019). The present paleobiogeographic study based on ruminants gives support to the direct Anatolian-Balkan ('Trans-Marmaran') dispersal pathway for hominins hypothesized by Ivanova et al. (2012), Spassov (2016) and Strait et al. (2016).

Conclusions

The Early Pleistocene community of ruminants from the Olteț River Valley shortly before the *Pachycrocuta* faunal turnover was dominated by local Pliocene holdovers *Rucervus* (*Arvernoceros*) *radulescui* and *Pliotragus ardeus*. *Gazellospira torticornis* and *Mitilanotherium inexpectatum* also have a long evolutionary history in southeastern Europe but attained a broader geographic distribution than *R. radulescui* and *P. ardeus*. Scarce remains of the primitive fallow deer *Dama eurygonos* from Valea Grăunceanului represent the oldest known record of this endemic species in southwestern Eurasia. The East Asian faunal elements are diverse (*Bison* (*Eobison*) sp., *Alces* sp., *Eucladoceros dicranios*, *E. ctenoides* and *Metacervoceros rhenanus*) but are represented by very few fossil remains. However, from the paleobiogeographic point of view, the Oriental ruminants from the Olteț River Valley indicate a zoogeographic connection with the geographically distant areas of Central Asia. The multivariate analysis associates the community of ruminants from the Dacian Basin with faunas from Eastern Europe and Central Asia as opposed to the biogeographically associated Transcaucasia, Mediterranean part of Europe and Western Europe. The composition of the ruminant assemblage from the Olteț River Valley mirrors the specific environmental and biotope conditions and may represent an accumulation of species mostly visiting a watering hole during the dry winter season in the riverine forest surrounded by more or less open plain landscape. Some of the species recorded in the mountainous area of the Dacian Basin, such as *Ovis*, *Hemitragus* and *Procamptoceras* from layer 13 of Kozarnika, are missing in the faunas of the Olteț River Valley.

The *Pachycrocuta* faunal turnover caused the extinction of the most of the Pliocene faunal holdovers from the Dacian Basin and triggered the dispersals of very large ruminants from southwestern Asia, such as *Praemegaceros obscurus* and *Megalovis latifrons*.

Mitilanotherium inexpectatum is the only exceptional case of survival of a Pliocene ruminant species in the Dacian Basin, probably due to its specific ecological niche that precluded ecological competition with newly arrived post-*Pachycrocuta* species. The distribution of *Eucladoceros* became confined to the refugia in Western Europe and the Italian Peninsula. The multivariate analysis reveals important paleobiogeographic transformations in southeast Europe and southwest Asia during the *Pachycrocuta* event that affected the Levant and the Dacian Basin. The Levant faunas lost their Afrotropical character and joined the Mediterranean and West European biogeographic regions. The Dacian Basin becomes a part of the Mediterranean paleobiogeographic zone. The mountain broad-leaved and mixed forests mark the biogeographic border between the warm Mediterranean paleobiogeographic area (including the Dacian Basin) and the inland dry continental zone with open plains and sparse woodland. Similar to the Iberian Peninsula and Transcaucasia, the Dacian Basin acted as a refugium for temperature-sensitive savanna ruminant species during the Early Pleistocene.

Acknowledgments

Many people helped with data collection and fieldwork and provided valuable advice: Eric Delson, Kieran McNulty, Silviu Constantin, Timothy Gaudin, Martha Tappen, Jenifer Hubbard, Ashly Romero, Caitlin Yoakum, Eric Mazelis, Samantha Gogol, Emil Ştiucă, Ionuţ Mirea, Razvan Arghir, Cristina Stan and Laura Văcărescu. We also thank the people of the Olteţ Valley and Tetoiu for their assistance during fieldwork and for initially locating many of these important fossils.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was generously supported by funding from the National Science Foundation (BCS-1636686), The Leakey Foundation, ‘Emil Racoviţă’ Institute of Speleology (ERIS), the Romanian Ministry of Research and Innovation through CNCS - UEFISCDI, grant PN-III-P4-ID-PCCF-2016-0016, and the EEA-Norway Grant #0126 (KARSTHIVES 2), Romanian Ministry of Education and Research, CNCS - UEFISCDI, project number PN-III-P4-ID-PCE-2020-2282, within PNCDI III (to V.D.), the Josiah Charles Trent Foundation and Duke University, the University of Arkansas, Ohio University and the University of California Santa Barbara. A part of research of R. Croitor was supported by the Gepkoski Grant (the Paleontological Society, USA; NSFNSF [BCS-1636686]; Romanian Ministry of Research and Innovation through CNCS-UEFISCDI [PN-III-P4-ID-PCE-2020-2282, PN-III-P4-ID-PCCF-2016-0016]; The Josiah Charles Trent Foundation and Duke University; Emil Racoviţă Institute of Speleology.

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