

PRELIMINARY DATA ON REINDEER FOSSILS FROM THE PALEOLITHIC SITE RAȘCOV-8 (EASTERN MOLDOVA) WITH REMARKS ON SYSTEMATICS AND EVOLUTION OF UPPER PLEISTOCENE REINDEER

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Abstract. The paper presents a morphological description of the reindeer fossils from the Upper Paleolithic site of Rașcov-8. The studied reindeer has relatively enlarged cheek teeth and small body size and is referred to the fossil subspecies *Rangifer tarandus constantini* FLEROV 1934. The studied material from Rașcov-8 represents the earliest occurrence of this subspecies in Moldova. *R. tarandus constantini* substituted *R. tarandus* cf. *guettardi* on the territory of modern Moldova ca. 19,000 – 20,000 years ago. Evolution, paleobiology, and systematics of the fossil reindeer are discussed.

Keywords: Reindeer, *Rangifer tarandus*, Late Pleistocene, systematics, evolution.

Rezumat. Studiu preliminar al renului din Stațiunea Paleolitică Rașcov-8 (Moldova de Est) cu observații asupra sistematicii și evoluției renului din Pleistocenul superior. Articolul prezintă descrierea morfologică a renului din așezarea paleolitică Rașcov-8. Renul studiat se caracterizează prin dinții relativ mari, dimensiuni ale corpului mici, și aparține subspeciei fosile *Rangifer tarandus constantini* FLEROV 1934. Materialul cercetat din Rașcov-8 reprezintă prima apariție a subspeciei studiate pe teritoriul Moldovei. Cu circa 19,000 – 20,000 ani în urmă *R. tarandus constantini* substituie *R. tarandus* cf. *guettardi* pe teritoriul actual al Moldovei. În articol se mai discută evoluția, paleobiologia și sistematica renilor fosili.

Cuvinte cheie: ren, *Rangifer tarandus*, Pleistocenul superior, sistematică, evoluție.

INTRODUCTION

Along with the wild horse and bison, the reindeer was an important hunted species of the Paleolithic man in Eastern Europe. The fossil remains of reindeer are abundant and represent in majority of cases kitchen waste of Paleolithic hunters. Some results on systematics, paleobiology, and evolution of the Paleolithic reindeer from Moldova and Western Eurasia are issued in my recent paper (CROITOR, 2010) in Russian. Here, I present a summary of my work on the European fossil reindeer, as well as a preliminary account on morphology and systematics of some reindeer fossils from Upper Paleolithic site Rașcov-8, not included in my previous work.

The fossils were unearthed by Dr. Serghei COVALENCO during 2006 field season from the third layer of the Upper Paleolithic site Rașcov-8. Rașcov-8 is situated on the left bank of the Dniester River, 12 km downstream from Camenca town (North-East of the Republic of Moldova). The third layer of Rașcov-8 yielded an archaeological complex of Epi-Aurignacian type (COVALENCO, *unpublished data*) and apparently, corresponds to the upper bed of Climăuți-2 (20,350±230 y. BC) and to Sagaidac-1 (21,240±200 y. BC) (CHETRARU et al., 2007; COVALENCO, *personal communication*). The fauna from the third layer of Rașcov-8 includes the following species: *Rangifer tarandus*, *Cervus elaphus*, *Equus caballus latipes*, *Mammuthus primigenius*, *Ursus arctos*. Reindeer is the best represented species of the sample.

MATERIAL AND METHODS

The sample includes fragments of cranial and postcranial bones, isolated teeth, a lower partially destroyed mandible, and three frontal bones with attached basal parts of antlers. The preservation of fossil remains is very poor, a lot being fragmented. In many cases, the mandibles are completely destroyed and only isolated cheek teeth are preserved. The pieces included in the present work are the following (bone ID includes the number of layer, square, and the number of bone): a right lower hemimandible 3A-E5-047 with M₂ and M₃ and isolated P₃ and P₄ which apparently belong to same specimen; a distal fragment of metatarsal bone 3A-E2"-012; isolated upper teeth M¹ and M² 3-E4-005; a row of upper molars M¹-M³ 3A-E5; two isolated frontal bones with attached basal parts of antlers 3A-E2"-009 that belong to the same individual; a frontal bone with basal part of antler 3A-E2"-010; a heel bone with destroyed proximal border 3A-E2"-008. The cheek teeth show an advanced wearing degree, some of premolars are completely worn, up to their roots.

The measurement of tooth row length in lower mandible is taken at alveoli. The upper tooth series length is measured at grinding surface. The length and breadth of the fourth premolar (P₄) crown are maximal. The height of pedicle is measured on the posterolateral side. Abbreviations used in text: DAP - anteroposterior diameter; DLM - lateromedial diameter; L - length; D - breadth; H - height.

Description

Family Cervidae GOLDFUSS 1820

Subfamily Capreolinae BROOKES 1828

Genus *Rangifer* H. SMITH 1827

Rangifer tarandus (LINNAEUS 1758)

***Rangifer tarandus constantini* FLEROV 1934**

The approximate breadth of the frontal constriction before pedicles of the frontal bones 3A-E2"-009 amounts to 114.5 mm. The pedicles are short, very robust, with rather incranial position on the skull. Both left and right antlers are characterized by the presence of well-developed basal tines. The second ramification of the right antler is situated about 65 mm from the basal ramification or about 88 mm from the antler base. The rest of measurements are quoted in table 1. The fragment of frontal bone with attached basal part of antler 3A-E2"-010 is badly damaged and for this reason measurements could not be taken. This specimen belongs to a smaller individual. Its antler is characterized by the presence of a strong basal tine.

Table 1. Measurements of teeth and bones of *Rangifer tarandus* from Raşcov -8.Tabel 1. Măsurători ale dinţilor şi oaselor de *Rangifer tarandus* de la Raşcov-8.

Specimen ID	Measurement	mm
Right pedicle 3A-E2"-009	DLM	37.8
	DAP	43.0
	H	12.3
Left pedicle 3A-E2"-009	DLM	40.6
	DAP	42.0
	H	16.8
Lower mandible 3A-E5-047	L P ₂ -M ₃	105.0
	L P ₂ -P ₄	47.7
	L M ₁ -M ₃	58.6
	H under P ₂	30.7
	D under P ₂	15.2
	L P ₄	17.8
	D P ₄	12.2
Series of upper molars 3A-E5	L M ¹ -M ³	60.0
Metatarsus 3A-E2"-012	DLM distal	40.0
	DAP distal	21.1
Calcaneus 3A-E2"-008	DLM distal	19.5
	DAP distal	27.6
	L tuberosity	61.8
	DLM sustentaculum	26.0
	DAP max	35.5

The mandible 3A-E5-047 is badly damaged, so only few measurements could be taken (Tab. 1). Since P₂ and M₁ miss, the measurements of the tooth series are taken with a certain approximation. The measurements of the lower tooth series are similar to the data on the reindeer from Brînzei-1 and Cosăuţi (Fig. 2A). Measurements of P₄ of the lower mandible 3A-E5-047 are larger than the sample from Raşcov-7, and fall within the variation range of P₄ from Brînzei-1 and Cosăuţi (Fig. 2B).

The series of isolated molars from the square 3A-E5 apparently belong to a single individual. The estimated value of the series of upper molars amounts to 60 cm and exceeds the maximal values of the sample from Cosăuţi. M¹ and M² have a weak cingulum-like structure on their lingual wall.

Unlike dental remains, postcranial bones are characterized by comparatively small sizes. The majority of postcranial bones of fossil reindeer show a clear size dimorphism. The distal epiphysis of metatarsal bone from Raşcov-8, which apparently belongs to a female, is close to the smallest specimens from Cosăuţi, and significantly smaller than the sample from Brînzei-1 (Fig. 2C). The length of tuberosity and the breadth of *sustentaculum tali* of the keel bone from Raşcov-8 are close to mean values of the samples from Raşcov-7 and Cosăuţi, being smaller than the similar bones from Duruitoarea Veche (Fig. 2D).

Comparatively large cheek teeth and small postcranial bones suggest that the reindeer from Raşcov-8 is rather close to the particular subspecies *R. tarandus constantini* from Cosăuţi, characterised by smaller body size and relatively and absolutely large cheek teeth.

DISCUSSIONS

At least three forms of fossil reindeer are found in Moldova: a large sized *Rangifer tarandus* ssp. from the third and fourth layers of Duruitoarea Veche (Early Paleolithic, ante-Mousterian Epoch) and a much younger reindeer from the second layer of Duruitoarea Veche (Magdalenian Epoch) and third layer of Brînzei-1 (31,000 – 28,000 y. BC *fide* ROGACHOV & ANIKOVICH, 1984), which is similar to the Lower Paleolithic reindeer and modern forest subspecies; a rather small-sized *Rangifer tarandus* cf. *guettardi* DESMAREST, 1822 from Raşcov-7 (19,000 – 19,500 y. BC *fide* CHETRARU et al., 2007), characterized by comparatively small teeth; and *Rangifer tarandus constantini* FLEROV 1934 from Cosăuţi (11,000 – 20,400 y. BC *fide* BORZIAC, 2008) and Raşcov-8. The relative size of cheek teeth represents the main diagnostic character of the enlisted reindeer forms. Cheek teeth of all fossil forms are significantly larger than teeth of modern reindeer. The difference of body size between various ecological forms of fossil reindeer, however, is not as sharp as in modern subspecies.

Rangifer tarandus ssp.

This is a large form of reindeer found in Duruitoarea Veche [layer 2 and Brînzeni-1 [3]. This is the largest form of fossil reindeer ever discovered in Moldova. The fragmentary character of the remains does not allow tracing any difference from the Lower Paleolithic reindeer from Duruitoarea Veche, at list in postcranial bones. Possibly, the reindeer from Duruitoarea Veche and Brînzeni-1 is an archaic form of reindeer that arrived in Europe during the earlier expansion events of the species. It equals in size the modern forest North American subspecies *R. tarandus caribou* and *R. tarandus terranova*. The fossil reindeer under discussion is characterized by rather long metapodials with narrow epiphyses, indicating possible adaptation to wooded landscape. Cheek teeth are larger than in modern *R. tarandus tarandus* (Fig. 2A). It seems that the sexual dimorphism in body size is stronger expressed than in other fossil reindeer: measurements of postcranial remains of females are broadly overlapping with data on females of smaller forms, while postcranial elements of males are particularly large (Fig. 2C, D). Possibly, the stronger pronounced sexual dimorphism in reindeer from Duruitoarea Veche and Brînzeni-1 is an adaptation to forested biotopes where reindeer males have to defend their territory and herd, so the larger size is an advantage in this case (GEIST, 1998). However, the influence of the selective strategy of Paleolithic hunters that pursued mostly largest males cannot be excluded. The remains of males consist 50% of the sample in Duruitoarea Veche [II] and 41% in Brînzeni-1 [III], therefore the presence of males in the samples is much higher than in a natural population and may indicate a hunting selection of the Paleolithic man (CROITOR, 2010).

An interesting shed antler from Duruitoarea Veche with destroyed distal portion (Fig. 3) needs a special discussion here. The antler is characterized by a strong branched basal tine resting right on the burr and a very high position of the second antler; the distance between the basal and the second tine amounts to 40 cm. Such a highly situated second tine is untypical for modern and majority known fossil Eurasian reindeer, which poses antlers with the basal and the second tines situated very close each to another and to the burr. The antler from Duruitoarea Veche in this respect resembles modern forest reindeer from North America. The stratigraphic position of this specimen is rather uncertain. DAVID (1980) assumed the Magdalenian age of the antler from Duruitoarea Veche, however, the antler could be older (CHETRARU, *personal communication*). It is difficult to give a firm interpretation of this antler. Possibly, the large archaic forest reindeer from Moldova resembled in its antler morphology to the North American forms and stands phylogenetically closer to caribou, however, one cannot exclude that this is just an individual variation of antler shape or an independently evolved character (CROITOR, 2010).

***Rangifer tarandus guettardi* DESMAREST 1822**

This form of reindeer was originally based on poor antler remains from the Paleolithic site Etampes in South France (DESMAREST, 1822). The antler shape resembles antlers of modern tundra reindeer. BOUCHUD (1967) ascribed to *R. tarandus guettardi* a complete skull associated with several postcranial bones from Foix (age ca. 7,100 y. BC). This reindeer is characterized by rather small cheek teeth; however, its muzzle is comparatively narrower than in modern reindeer: index [height at *rhynion* / breadth at P²] amounts to 68.6% in the specimen from Foix that is quite narrow if compared to 81.9% in modern *R. tarandus groengandicus*. Long bones of the reindeer from Foix are rather short with narrow epiphyses like in modern tundra reindeer. Taking in account the reindeer from Foix, BOUCHUD (1967) suggested that the fossil reindeer of Europe represented a tundra ecological form. A similar small-sized form with rather small dentition was reported by VALLI & GUÉRIN (2000) from Jaurens (France, absolute age 29,300 – 32,600 y. BC). The shape of the antlers from Jaurens is similar to modern tundra reindeer: the second tine is situated very close to the basal tine, which in its turn rests on the burr; the palmation in distal part of the antler is not developed (VALLI & GUÉRIN, 2000: Fig. 3, pl. 2, Fig. 1). BELAN (1983) and SABLIN & KUZMINA (1992) ascribed all fossil reindeer from Eastern Europe to *R. tarandus guettardi*, but apparently this is a simplified solution. Only the reindeer from Rașcov-7 shows certain affinity to small-sized reindeer of Western Europe: it is characterized by smaller postcranial bones with narrower diaphyses, proportionally diminished cheek teeth, and less pronounced sexual dimorphism (CROITOR, 2010). The second antler tine is situated very close to the basal tine as in modern Eurasian subspecies. Because of the extremely fragmentary character of the remains of the reindeer from Rașcov-7, it is better to assign it as *R. tarandus cf. guettardi*, since the resemblance to the reindeer from Western Europe could be superficial.

BOUCHUD (1967) referred to *R. tarandus guettardi* a large form of reindeer from Villestoft (Danmark) characterized by long metapodials, large hypertrophied antlers with palmed basal tines and distal portion of antlers, rather small cheek teeth, and relatively narrow skull and its facial part: the index [height at *rhynion* / breadth at P²] amounts to 58.0%. Extremely large body size, palmed antlers, and small cheek teeth may suggest that the reindeer from Villestoft is similar to modern forest reindeer *R. tarandus fennicus*; however its cranial shape is peculiar: nasal bones are rather similar to nasal bones of modern tundra reindeer according to the morphological characters indicated by LÖNNBERG (1909), while the facial part of skull is narrow as in fossil subspecies. The systematical position of the reindeer from Villestoft is not clear yet.

***Rangifer tarandus constantini* FLEROV 1934**

FLEROV (1934) proposed a new species name *R. constantini* based on an almost complete skull (the specimen is now lost) of fossil reindeer from the Paleolithic site of Malta (ca. 16,000 y. BC *fide* BOUCHUD, 1967), Irkutsk Region, Siberia. Unlike modern reindeer, the reindeer form from Malta was characterized by enlarged cheek teeth, large lower incisors, and narrow muzzle with index [height at *rhynion* / breadth at P²] amounting to 57.9% (FLEROV, 1934), short limb bones with broad epiphyses (ERMOLOVA, 1978). The antlers of *R. tarandus constantini* are rather long, with the

second tine situated close to the basal tine, which, in its turn, is situated close to the burr. The distal portion of antler is not palmed and ended with four posterior crown tines; a small posterior tine is present. The similar large-toothed form of reindeer was found in Kostenki (20 000 – 30 000 y. BC), Russia (SABLIN & KUZMINA, 1992), various Paleolithic sites from Ukraine (BELAN, 1983), and Cosăuți (CROITOR, 2010; Fig. 2A, Fig. 4). Apparently, the remains of *R. tarandus constantini* from Rașcov-8 represent the earliest record of this subspecies in Moldova. AUJARD-CATOT et al. (1979) described as *R. tarandus tarandus* an interesting almost complete skeleton of reindeer from the late Würmian site l'Aven des Planes, France. The large size of upper cheek teeth is the most remarkable character of this reindeer: the length of M¹-M³ series amounts to 56.5 mm and is comparable to the largest specimens of the sample from Cosăuți (L M¹-M² ranges from 50.4 to 58.0 mm: DAVID et al., 2003). Postcranial remains of the reindeer from l'Aven des Planes are quite similar to the material from Cosăuți. In my opinion, the reindeer from l'Aven des Planes should be ascribed to *R. tarandus constantini*.

R. tarandus constantini represents an extreme adaptation of reindeer to grazing in open dry periglacial plain environment. Possibly, food habits of this subspecies were similar to fossil reindeer from Alaska that displayed a heavy occlusal tooth wear for young and adult animals that reflects a very abrasive diet (RIVALS & SOLOUNIAS, 2007). Unlike modern reindeer, the volume of the nasal cavity of *R. tarandus constantini* is rather small that suggests that the Paleolithic reindeer did not evolve yet adaptations to cold air breathing (FLEROV, 1952). The function of increased nasal cavity is air warming and moistening before its entrance to the trachea and lungs. Nasal cavity is correlated with muzzle breadth and the maximal volume of the nasal cavity is recorded in the modern arctic reindeer (FLEROV, 1952; SOKOLOV, 1995).

Reindeer in Paleolithic Art of Western Europe

GEIST (1998) regards the famous engraved sketch of the reindeer from Kessler-Loch (near Tayngen; about 11,000 y. BC), Switzerland, as a classic European tundra reindeer. The antlers of figured reindeer have small palmations on the ice tine (basal tine), second tine and on the distal portion of antler (Fig. 5B). The back of reindeer is dark, as well as the frontal parts of the anterior legs and the posterior limbs, the white rump patch is large, the white neck with long neck mane, the withers are white, and the flank dark strip is present. Such a pattern of coat coloration is characteristic to modern tundra reindeer *R. tarandus tarandus* (FLEROV, 1952; GEIST, 1998). A similar coat pattern is found in the reindeer figured in Les Trois-Frères (12,000 y. BC), France (Fig. 5A). However, the coat coloration of the couple of reindeers figured in Font de Gaume (17,000 y. BC), France, is different. The body of the reindeer from Font de Gaume is dark, including withers and forelimbs. The rump patch is not indicated. The neck is white contrasting with the dark body and legs. The light flank strip is clear in one case and is hardly visible in another figure (Fig. 5C). Such a pattern of coat is characteristic to modern forest subspecies of reindeer from Southern Siberia *R. tarandus angustirostris* (FLEROV, 1952). The image of the reindeer from Font de Gaume possibly represents an archaic population of forest reindeer that survived in Western Europe before the last glaciation.

Some Remarks on the Evolution of the Paleolithic Reindeer

The origin of reindeer is associated with North American continent or Beringia (FLEROV, 1952; GEIST, 1988). According to GEIST (1998), the first immigration event of reindeer in Eurasia occurred during the Riss Glaciation. The earliest expansion of reindeer is documented in Süßenborn (Germany) where *Rangifer arcticus stadelmanni* was recorded (KAHLKE, 1969). BOUCHUD (1967) indicating a certain affinity of the reindeer from Süßenborn with modern barren ground caribou from North America. GEIST (1998) regards the barren ground caribou as a forerunner for all modern Eurasian subspecies of reindeer. The genetic gap between the tundra subspecies *R. tarandus tarandus* and the forest subspecies *R. tarandus fennicus* is not as large as in the case of North American forest caribou and barren ground caribou (*ibidem*). According to the analysis of mitochondrial DNA, the modern Eurasian tundra and forest subspecies have diphyletic origin from a smaller refugia in western Eurasia situated in close connection to the extensive ice sheet that covered Fennoscandia, and a larger refugia of Beringia (RØED, 2005). Our palaeontological data support this conclusion: apparently, the origin of *R. tarandus guettardi* took place in the smaller Western refugia, while *R. tarandus constantini* is the reindeer form related to the Beringian refugia. During the last glacial maximum, *R. tarandus constantini* substituted *R. tarandus* cf. *guettardi* in Moldova and continued its expansion westward to France. The maximal area of distribution of the latter subspecies ranged from Baikal area to Western Europe.

RANKAMA & UKKONEN (2001) suggest that Western Europe is the area of origin of modern tundra reindeer. Possibly, the reindeer from Villestofte is a transitional form between the large-toothed Upper Pleistocene reindeer and the modern *R. tarandus tarandus*. Specific adaptations of *R. tarandus fennicus* to forest habitats evolved quite recently after forest extension in postglacial time and have a secondary character (GEIST, 1998; RØED, 2005). According to RANKAMA & UKKONEN (2001), the origin of forest reindeer could be related to forested refugia in the East from Fennoscandia. Possibly, this hypothesis finds a support in ALEKSEEVA (1990), who mentioned a fossil skull of reindeer similar to *R. tarandus fennicus* discovered in Tatarstan and stored in the Zoological Institute (Sankt-Peterburg).

CONCLUSIONS

R. tarandus constantini is a subspecies of Eastern origin and represents the last expansion event caused by Würmian (Weichsel) glaciation from the large species refugia situated in Beringia. This fossil reindeer represented an open landscape ecotype similar to modern tundra reindeer, distinguished from modern subspecies by extreme for a

reindeer grazing adaptations and comparatively small volume of nasal cavity. The fossil remains from Rașcov-8 represent the earliest occurrence of *R. tarandus constantini* in Moldova. *R. tarandus constantini* arrived on the territory of modern Moldova about 19,000–20,000 years ago and substituted *R. tarandus* cf. *guettardi* characterised by comparatively small cheek teeth (which, however, are still larger than in modern reindeer). By the end of Würmian glaciation, *R. tarandus constantini* reached France and its area of distribution ranged from Eastern Siberia to Western Europe. Taking into consideration RØED's (2005) suggestion of diphyletic origin of modern Eurasian subspecies of reindeer, both *R. tarandus constantini* and *R. tarandus guettardi* contributed to the origin of modern *R. tarandus tarandus* and *R. tarandus fennicus*. Climate warming and extension of forest over the largest part of Eurasia caused the displacement of reindeer's area of distribution northward into tundra and forest-tundra and the subsequent evolutionary selection for soft and nutritious forage and breathing cold and dry air. Unlike fossil *Rangifer*, modern subspecies of reindeer of Eurasia are concentrate feeders with small cheek teeth and reduced lower incisors and canines that do not participate in food gathering (modern reindeer take the forage by lips) and have enlarged nasal cavity and specific anatomical adaptations to breathing cold and dry air (FLEROV, 1952; SOKOLOV, 1995).

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FIGURES

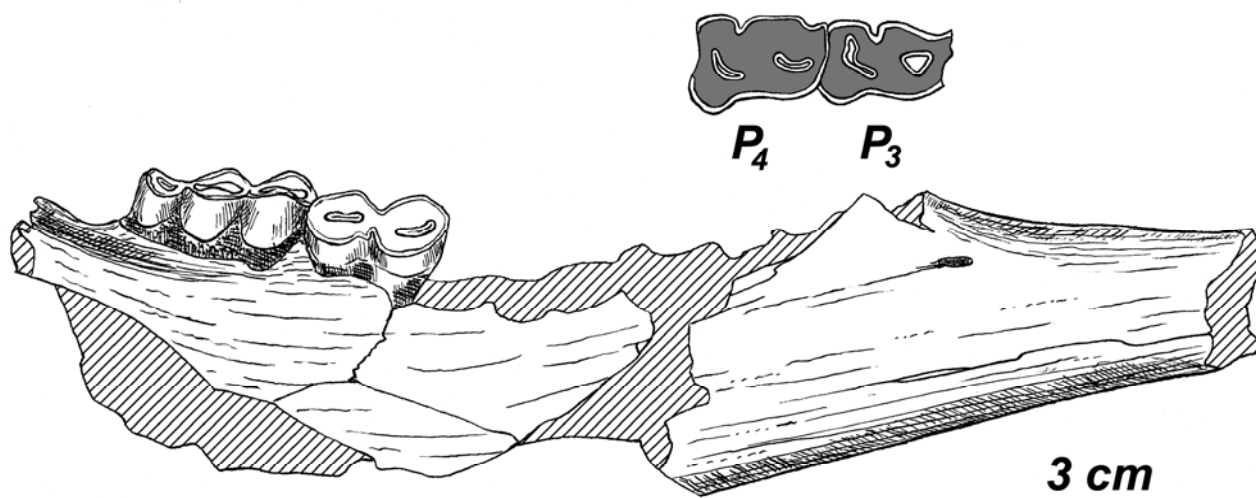


Figure 1. Mandible 3A-E5-047 of *R. tarandus constantini* from Raşcov-8.
 Figura 1. Mandibula 3A-E5-047 de *R. tarandus constantini* de la Raşcov-8.

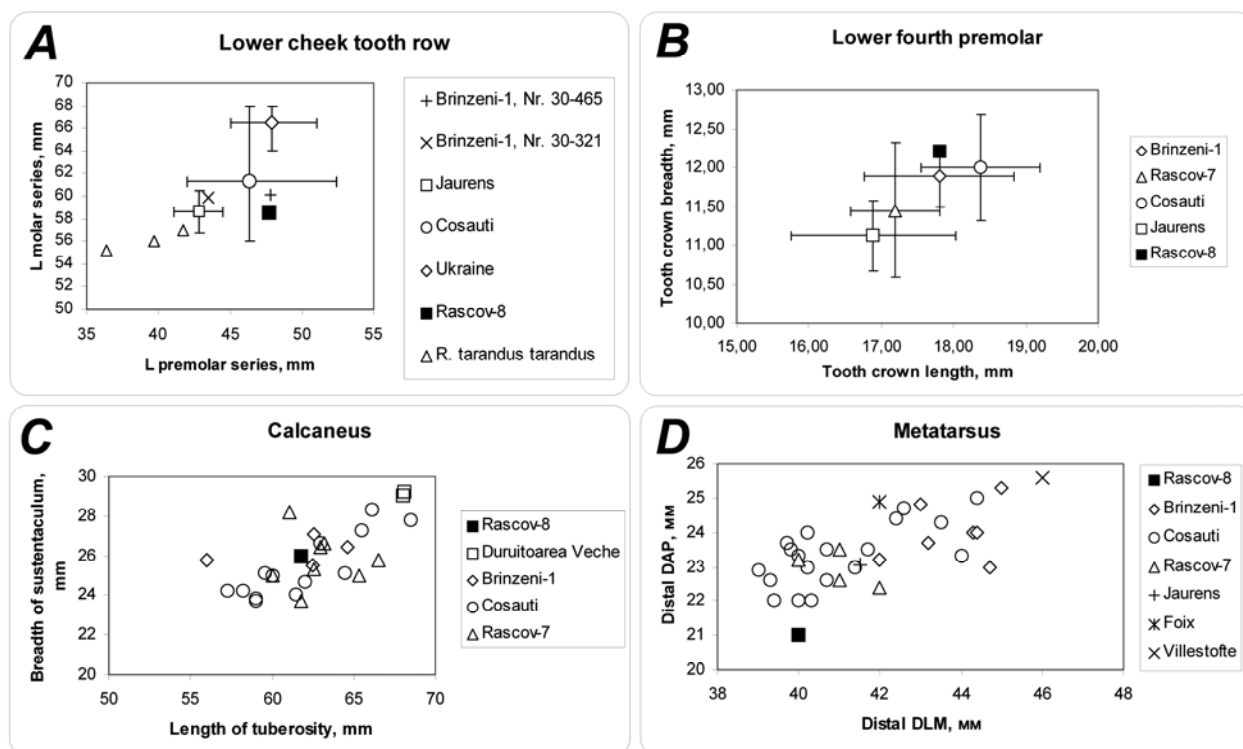


Figure 2. Measurements of fossil remains of *R. tarandus constantini* from Raşcov-8 compared with modern and fossil forms of reindeer: A, lower cheek tooth series; B, lower fourth premolar (P_4); C, keel bone; D, metatarsal bone (data from Jaurens are adapted from VALLI & GUÉRIN, 2000; data from Ukraine are from BELAN, 1983; data on fossil reindeer from Raşcov-7, Duruitoarea Veche, Brinzeni-1, Cosăuți, and modern *R. tarandus tarandus* are from CROITOR, 2010).

Figura 2. Măsurători ale resturilor fosile de *R. tarandus constantini* de la Raşcov-8 comparativ cu formele moderne și fosile de ren: A, serie de dinți inferiori A, lower cheek tooth series; B, al patrulea premolar inferior (P_4); C, keel bone; D, osul metatarsian (date de la Jaurens adaptate după VALLI & GUÉRIN, 2000; date din Ucraina după BELAN, 1983; datele privind renii fosili de la Raşcov-7, Duruitoarea Veche, Brinzeni-1, Cosăuți și renul modern *R. tarandus tarandus* sunt după CROITOR, 2010).

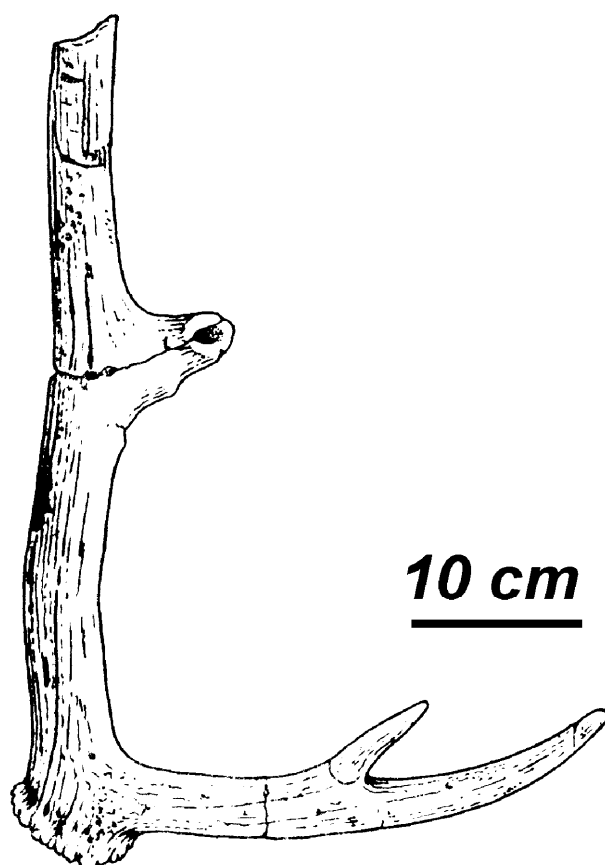


Figure 3. The shed antler of reindeer from Duruitoarea Veche (adapted from DAVID, 1980).
Figura 3. Corn de ren de la Duruitoarea Veche (adaptat după DAVID, 1980).

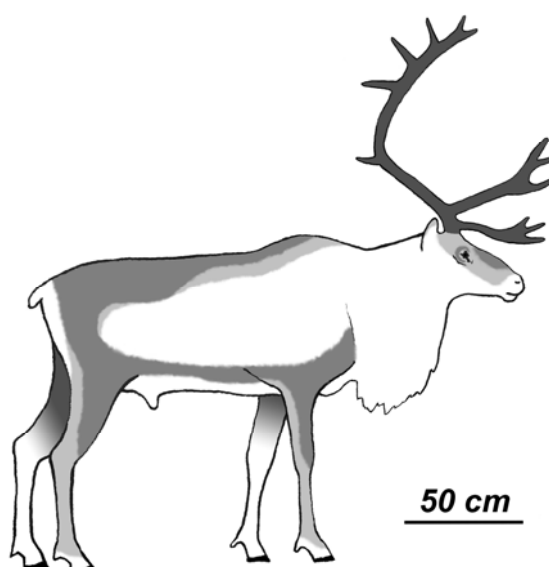


Figure 4. Reconstruction of the fossil reindeer *Rangifer tarandus constantini* from Moldova (based on antler fragments from Cosăuți and the engraved figure of reindeer from Kessler-Loch, Switzerland).
Figura 4. Reconstituirea renului fosil *Rangifer tarandus constantini* din Moldova (bazată pe fragmentele de corn de la Cosăuți și pe desenele cu reni de la Kessler-Loch, Elveția).

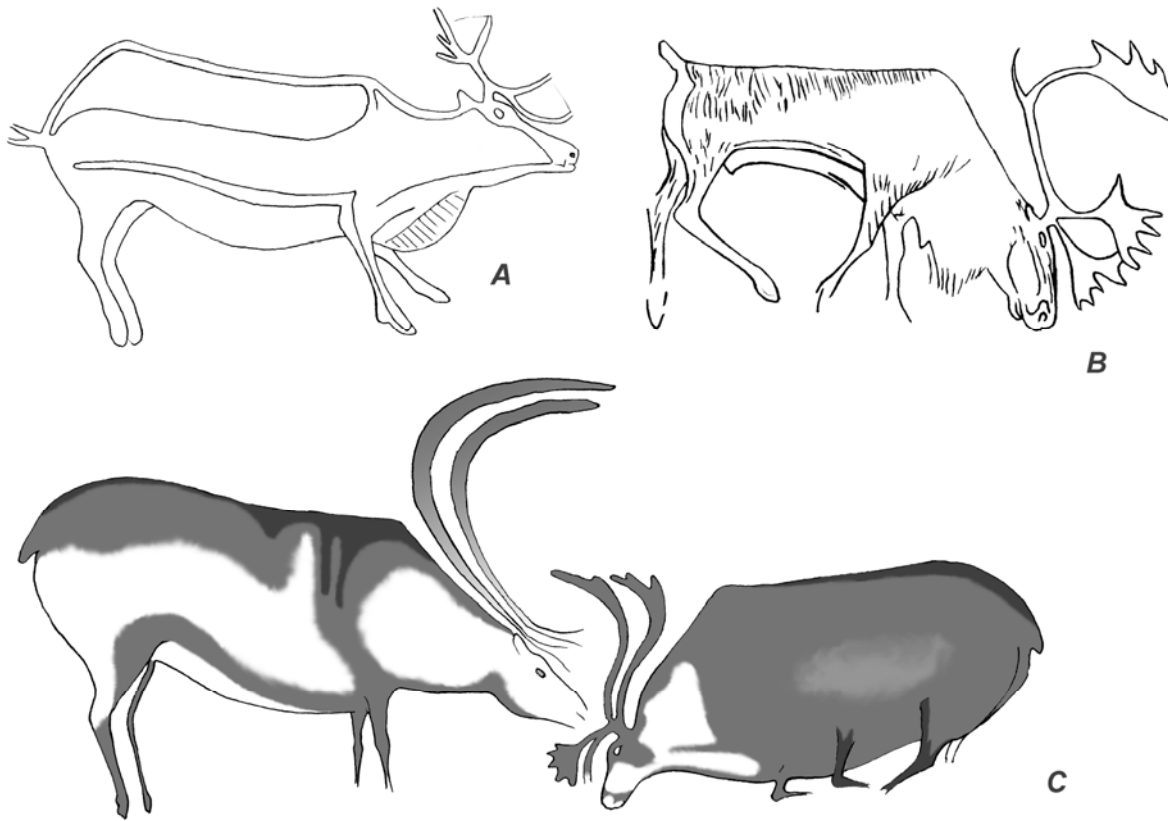


Figure 5. Paleolithic images of reindeer: A, Les Trois-Frères (adapted from LEROI-GOURHAN, 1965); B, Kessler-Loch (adapted from MERK, 1876); C, Font de Gaume (adapted from MONGAIT, 1973).

Figura 5. Imagini paleolitice de ren: A, Les Trois-Frères (adaptat după LEROI-GOURHAN, 1965); B, Kessler-Loch (adaptat după MERK, 1876); C, Font de Gaume (adaptat după MONGAIT, 1973).

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