

## SYSTEMATICAL POSITION AND EVOLUTION OF THE GENUS *ARVERNOCEROS* (CERVIDAE, MAMMALIA) FROM PLIO-PLEISTOCENE OF EURASIA

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**Abstract.** The article presents a description of new fossils of *Arvernoceros ardei* from the Pliocene of Southern Moldova, followed by an overview on the important data regarding the representatives of the genus *Arvernoceros* from Plio-Pleistocene of Europe and their relationship with Asian fossil cervids. The comparative study of antler morphology suggests a close relationship of *Arvernoceros* with modern genus *Rucervus*.

**Keywords:** *Arvernoceros*, Cervidae, Plio-Pleistocene, Eurasia, systematics, evolution.

**Rezumat. Poziția sistematică și evoluția genului *Arvernoceros* (Cervidae, Mammalia) din Plio-Pleistocenul Eurasiei.** Articolul prezintă descrierea materialului nou al cerbului *Arvernoceros ardei* din Pliocenul Moldovei Meridionale și sinteza datelor relevante privitoare la genul *Arvernoceros* din Pliocenul și Pleistocenul Europei, precum și relațiile cu formele fosile asiatice. Analiza comparativă a morfologiei coarnelor sugerează o relație filogenetică apropiată între *Arvernoceros* și genul actual *Rucervus*.

**Cuvinte cheie:** *Arvernoceros*, Cervidae, Plio-Pleistocen, Eurasia, sistematică, evoluție.

### INTRODUCTION

HEINTZ (1970) created the genus *Arvernoceros* with a single species *Cervus ardei* CROIZET & JOBERT from the Lower Villafranchian site Perrier-Etouaires (France), with unusual traits in antler morphology, such as a generally simple antler pattern with two axes, and a well developed distal palmation of antler. HEINTZ (1970) associated some isolated upper molars with cyngulum, claiming the hypothetical ancestral relationship of *Arvernoceros* with *Megaloceros*.

For a long time, the genus *Arvernoceros* was considered to be a peculiar Lower Villafranchian element of restricted geographical value. However, the later publications significantly broadened the geographical and stratigraphic distribution of the genus. VISLOBOKOVA & CHANGKANG (1990) mentioned the presence of the genus in Early Pliocene of Mongolia. BAJGUSHEVA (1994) reported *Arvernoceros* sp. from Livenzovka (South Russia, Azov Sea shore). In 1992, DAVID established the new large sized species *Arvernoceros verestchagini* (Fig. 2) based on a shed antler from the upper deposits of a quarry near the village of Salcia (Moldavia). The Salcia deposits have yielded a fauna of Middle-Upper Villafranchian type (ABBAZZI et al. 1999), indicating the presence of the genus *Arvernoceros* in younger biostratigraphic levels than previously suggested. The giant *Arvernoceros verestchagini* from Salcia apparently is very close to a large deer from Apollonia (Latest Villafranchian, Greece; CROITOR & KOSTOPOULOS, 2004) and possibly is a junior synonym of *Pseudalces mirandus* FLEROW 1962 (CROITOR, 2005a, b) from the mixed Villafranchian fauna from the Kosiakinskij quarry (Northern Caucasus foothills). *P. mirandus*, according to International Zoological Code, are still available species and genus names and cannot be regarded as a *nomen oblitum*. The taxonomical difficulty comes from the poor preservation of the type specimen of *Pseudalces mirandus*, which is represented by an orbito-frontal cranial fragment with right upper molar series, which did not preserve the diagnostic characters used in description of *Arvernoceros*.

CROITOR & KOSTOPOULOS (2004) proposed a revision of the genus with emended definition and enlarged genus composition. According to the new definition, cingulum in upper molars is not considered as a diagnostic character for the genus. Beside the type species *A. ardei* and giant *A. verestchagini*, CROITOR & KOSTOPOULOS (2004) also included in this genus KAHLKE's (1997) *Eucladoceros giulii*, which is characterized by remarkably long and slender limbs, simple teeth patterns without cingulum, and the typical for *Arvernoceros* pattern of antler construction, which can be noted in a single well-preserved juvenile antler.

The systematic position of *Arvernoceros* is still unclear. TEILHARD DE CHARDIN & PIVETEAU (1930) assumed that *Cervus ardeus* is rather close to modern *Elaphurus*. LISTER (1987) considered *Arvernoceros* as a tribe *incertae sedis* genus. VISLOBOKOVA (1990), following the HEINTZ's (1970) hypothesis on phylogenetic relationship between *Arvernoceros* and *Megaloceros*, included the former genus in the tribe Megacerini. DI STEFANO & PETRONIO (2000-2002) suggested that *Arvernoceros ardei* is closely related to *Axis shansius*, and therefore they regarded *Arvernoceros* as a junior synonym of *Axis*.

In the present article, a description of the first find of *Arvernoceros ardei* in Moldova and Eastern Europe is presented, as well as a discussion of the systematic position, radiation and evolution of the genus.

## MATERIAL AND METHOD

The new fossil cervid antler fragments described in the present study were collected from the close vicinity of Slobozia Mare village, Cahul District, Southern Moldova (Fig. 1). The fossils had been discovered by Vasile Constantin BRÎNZĂ in the outcrops situated southeast of Slobozia Mare, in the place called “Rîpa de la Ganu”. The unlabeled fossils are curate at the Village Museum of Slobozia Mare. The sample from Rîpa de la Ganu includes also few poor remains (two basal antler fragments and a calcaneus with damaged surface) of a smaller deer. The systematic attribution of those poorly preserved bones is undeterminable, since the outcrops near Slobozia Mare has yielded another cervid form *Dama* sp. (CROITOR, 2006). An advanced and rather small-sized *Anancus arvernensis* is also recorded in the neighbourhoods of Slobozia Mare, which, according to Theodor OBADĂ (*personal communication*) may indicate that these deposits belong to Middle Villafranchian (MN17). However, the exact stratigraphic position of many finds stored in the Museum of Slobozia Mare is unknown, therefore one cannot assume that the taxa discovered in the outcrops near Slobozia Mare represent a genuine mammalian assemblage.

The fossil sample of *Arvernoceros ardei* from the type locality Perrier-Etoudaires (France) is used in the present study as a comparative material. The material from Perrier-Etoudaires had been revised and described in details by HEINTZ in 1970 and at present, a part of material is stored in the National Museum of Natural History in Paris, and another part in the Palaeontological Museum of the University of Lyon (France). The osteological material of modern deer used in the comparative study is stored in the Zoological Museum “La Specola” of the University of Florence (Italy). The proposed body mass estimations are based on the cranio-dental measurements according to the method of JANIS (1990).

**Description**

Family Cervidae GOLDFUSS, 1820

Subfamily Cervinae GOLDFUSS, 1820

Genus *Arvernoceros* HEINTZ, 1970

*Arvernoceros ardei* (CROIZET & JOBERT, 1828)

The studied specimen is a right shed antler with a damaged distal part and a broken off basal tine (Fig. 2). The length of the preserved part of the beam amounts to 25 cm. The antler beam is cylindrical, set obliquely on the burr and directed sideward and backward. The antler slightly turns back at the level of first ramification then the antler beam is gently curved upward and becomes almost straight, with slight undulation. The first ramification is situated high above the burr. The basal tine is flattened and set obliquely with respect to the antler beam. The antler beam generally is cylinder-shaped; however, there is a longitudinal blurred keel on the anterior side of the proximal portion of the beam. The transversal cross-section of the beam is oval above the first tine and regular circular (anteroposterior diameter amounts to 27.0 mm; lateromedial diameter, 28.0 mm) at the level of breakage. The rest of measurements are indicated in the table. The beam surface is covered with longitudinal ridge-and-furrow ornament. The antler from Slobozia Mare is somewhat smaller than the neotype of *Arvernoceros ardei* from Perrier-Etoudaires, however, the shapes of antler base and of antler beam, as well as the flattened set obliquely basal tine in the antler from Moldova are characteristic of *Arvernoceros ardei*.

The distal fragment of the right antler represents a bifurcation with two tines situated in the parasagittal plane. The length of the fragment amounts to 176 mm. The antler is strongly compressed from the sides in the area of the ramification. The cross-section of the posterior tine is regularly circular. The angle of ramification amounts to 47°.

## DISCUSSION

*Arvernoceros ardei*. The species was firstly described by CROIZET & JOBERT (1828) as *Cervus ardeus* from the Early Villafranchian of Perrier-Etoudaires. Later, HEINTZ (1970) placed it in the separate monotypic genus *Arvernoceros*. This is a rather large deer with estimated body mass amounting to 180 kg (the body mass estimation is based on the mixed *perrieri-ardei* sample described by HEINTZ, 1970). This deer is interesting by its mixture of some primitive characters (long parallel pedicles trended backwards; simple antler plan corresponding to three-pointed evolutionary stage; primitive dentition with simple P<sub>4</sub> and relatively long premolar series) and such advanced characters as large body size and distal antler palmation that appears in mature males (Fig. 3, C). The shape of distal palmation of the type specimen with three tines pointed forwards, possibly, is not typical and the reconstruction of two distal tines may not be exact. The distal fragment of the antler PET1024 from Perrier (the National Museum of Natural History, Paris) suggests that the palmation was bilobed, with two prongs on the one of the preserved lobe of palmation, and apparently, evolved from a simple distal fork. A similar shape of palmation is found on the antler fragment from the Upper Pliocene site of Valea Grauncianului (Fig. 3, D, Institute of Speleology, Bucharest), which belongs to somewhat larger form similar to *A. ardei* (CROITOR & POPESCU, work in progress). The basal tine is often supplemented with an accessory prong in fully grown large antlers (Fig. 3, C1). *A. ardei* is peculiar since it represents for the first time in cervid history an ecomorphological large-sized form with palmed antlers. Somewhat later, by the end of Pliocene this ecological space will be conquest by *Cervalces gallicus*, and then, in Pleistocene, a large variety of large cervids with palmed antlers belonging to various unrelated evolutionary lineages (genera *Praemegaceros*, *Megaloceros*, *Sinomegaceros*, *Alces*, *Dama*) will occur in Northern Eurasia. The ecomorphological significance of palmed antlers is a

matter of debates, but generally their important social function is assumed (GEIST, 1998). In my opinion, the thermoregular function of growing antlers suggested by STONEHOUSE (1968) may be another important factor favouring the development of palmations in large-sized deer inhabiting open landscapes with continental and seasonal climate with hot summers. Growing antlers are rich in blood vessels and represent an effective organ of thermoregulation. Apparently, palmed antlers are characterized by an increased surface of hit radiation. It is important to note that all large-sized deer with palmed antlers appeared in high latitudes with continental climate. There are no cervids with palmed antlers that evolved in tropical or subtropical environments<sup>1</sup>. One can assume that *A. ardei* was a first Cervinae that evolved some adaptations to more open landscape, most probably an open woodland or wooded savannah, since its teeth are still quite primitive. The earliest record of *Arvernoceros* in Europe was reported from Late Ruscian (Early Pleistocene) of Węże-1 (Poland); this is a frontal part of skull, which shows similarity with the frontal shape of *A. ardei* from Perrier-Etoudaires (CROITOR & STEFANIAK, 2009). A few remains from Pliocene site Węże-2 (Poland) ascribed to *Arvernoceros* (STEFANIAK, 1995), in fact, are poor and their systematic determination is not possible. *A. ardei* was reported by HEINTZ (1970) from several Lower Villafranchian sites of France and Spain. The antler from Slobozia Mare is the first specimen originating from Pliocene of Eastern Europe that can be ascribed to *A. ardei* with a certain confidence.

***Arvernoceros ubensis*.** This deer from Upper Pliocene of Altai, South of Western Siberia, was originally described by VISLOBOKOVA (1977) as *Cervus ubensus* (Fig. 3, A). Later, she placed this species in the genus *Axis* (VISLOBOKOVA, 1990). Actually, the antler shape of the deer from Altai suggests a close relationship with *Arvernoceros ardei*. This is a rather large deer (140 kg) with primitive dentition ( $P_4$  simple, premolar series relatively long, devoid of cingulum and additional enamel folds in upper molars). Antler morphology is very remarkable and strikingly reminds some of the morphological variants of *A. ardei*. Antlers are three-pointed, with one basal tine forming an obtuse angle with the beam ( $102^\circ$ ), and a distal fork. The basal tine is flattened and supplemented with an accessory prong on its upper side. The antler beam is cylindrical, with a faint keel on the anterior side above the first ramification, and flattened distal portion preceding the distal fork. The antler morphology of *Arvernoceros ubensis* reminds the specimen from Slobozia Mare, however, unlike the antler from Moldova, the basal tine in *A. ubensis* is situated close to the burr and it forms an obtuse angle. Unlike *A. ardei*, pedicles of *A. ubensis* are quite short (pedicle transversal diameter exceeds pedicle length); however, their parallel orientation and close position on the skull are the same as in *A. ardei*.

***Arvernoceros giulii*.** This is a large-sized deer from Untermassfeld (Lower Pleistocene, Germany) originally described by KAHLKE (1997) as *Eucladoceros giulii*. This is a large-sized deer with body mass attaining 400 kg. Unusually long metapodials are the most peculiar character of this species (KAHLKE, 1997). The dentition, as in previous species, is quite primitive, with simple  $P_4$ , relatively long lower premolar series and upper molars without cingulum. The complete adult antlers of *A. giulii* are not known. The hypothetical reconstruction of the antler proposed by KAHLKE (1997: fig. 28) is based on scant fossil fragments belonging to individuals of different ontogenetic ages and probably different species, therefore the eucladocerine comb-like structure provided is not fully supported (CROITOR & KOSTOPOULOS, 2004). The juvenile antler from Untermassfeld figured by KAHLKE (1997: fig. 26, p. 229) represents a typical for *Arvernoceros* antler shape with flattened first tine ended with a fork and a distal dichotomous branching. Apparently, to this species it should be ascribed a lower mandible from Early Pleistocene of Cișmichioi (Moldova) reported earlier as *Arvernoceros* sp. (CROITOR, 2005 b). Lower mandibles from Rosieres (France) of a large-sized deer described by STEHLIN (1912) as *Cervus (Megaceros) dupuisi* (now should be regarded as *nomen oblitum*) also belong to the species under discussion. Most probably, the frontlet of a large deer from Early Pleistocene of Saint-Prest (France) reported by GUERIN et al. (2003) as *Praemegaceros verticornis*, in fact, belongs to *A. giulii*.

*A. giulii* was a large-bodied long-legged open-landscape runner that inhabited wooded savannah. Unlike *Praemegaceros*, which also appears in Europe in Early Pleistocene, *A. giulii* maintains a primitive morphology of dentition suggesting that this deer was a browser.

***Arvernoceros verestchagini*.** This is an extremely large species (body mass ca. 700 kg), probably, the largest among Cervinae, with rather simple shape of antlers (Fig. 3, B). The holotype, a single known antler from Villafranchian of Salcia (Moldova), is similar to *A. ardei*, but it is larger and lacks distal palmation (DAVID, 1992). The antler ends with a simple distal fork. The basal tine is strong, extended into a small palmation with three prongs. The remains of similar large cervids from Villafranchian of Kosiakinskij Quarry (Russia) and Latest Villafranchian of Apollonia (Greece) provide us with some information about the ecomorphology of this species. The giant *Arvernoceros* maintains rather long pedicles, well-developed preorbital fossae, primitive dentition with simple  $P_4$ , however, the lower premolar series is quite short (CROITOR & KOSTOPOULOS, 2004). Limb bones are quite long for such a heavy animal, but also the proportions of limbs are unusual. The length of metacarpals approaches that of metatarsus and radius reminding the postcranial proportions of some browsing giraffids. Perhaps, the extremely long limb bones of *A. cf. verestchagini* from Apollonia in combination with primitive morphology of dentition portray this deer as a high-lever browser that feed on the tree-crown leaves, occupying an ecological niche similar to that of modern giraffes (CROITOR & KOSTOPOULOS, 2004).

<sup>1</sup> The natural area of distribution of modern rather small-sized fallow deer with palmed antlers *Dama dama* and *D. mesopotamica* is restricted to rather warm lands of Anatolia and Persia; however, the palmed antlers first appeared in large-bodied Middle Pleistocene *D. clactoniana* from Western Europe.

***Arvernoceros bifurcatus*.** TEILHARD DE CHARDIN & PIVETEAU (1930, pl. VIII, Fig. 10) described their species *Cervus (Elaphurus) bifurcatus* from the Early Pleistocene of Nihowan (China). According to these French authors, the antler morphology of the deer from Nihowan is close to modern *Elaphurus*, but also reminds “*Cervus*” *ardeus* (= *Arvernoceros ardei*). The antler of *Arvernoceros bifurcatus* is characterized by a high position of first tine which is terminated by a fork. The antler beam bends toward posterior in the area of the first ramification, then it curves forward and forms a distal bifurcation. Teeth, skull and postcranial bones are unknown.

**Remarks on systematics and evolution.** The deer of the genus *Arvernoceros* display quite conservative little varying morphology of antlers, but also very conservative morphology of dentition. The antlers generally remain simple tree-pointed, with high position of basal tine and a distal fork. The basal tine often tends to be flat and is supplemented by an additional prong. The advanced condition of first tine shape is found in *A. bifurcatus* (fork-shaped) and *A. verestchagini* (palmed with three prongs). Distal portion of antler is usually terminated by a simple fork, but in some European forms (*A. ardei*) the distal part of antler is extended into a small palmation. The pattern of antler construction of *Arvernoceros* corresponds to modern *Rucervus duvauselli* (Fig. 3, E), which evolves antlers with dichotomous pattern of distal crown ramification and basal tine with additional prong occasionally present. According to genetic studies carried out by PITRA et al. (2004), the modern genus *Rucervus* together with *Axis* is a Late Miocene off-shoot of Cervinae phylogenetical stock. Therefore, the appearance of *Rucervus*, likely, is a part of the first radiation of Cervinae that produced Early Pliocene *Arvernoceros ardei* and “*Cervus*” *warthae* in Europe (CROITOR & STEFANIAK, 2009). The earliest fossil record of *Rucervus* known so far was reported from Late Pliocene of Siwalik Hills (AZZAROLI, 1954). Apparently, the extinct genus *Arvernoceros* is phylogenetically close to modern *Rucervus*. At the present state of knowledge, it is difficult to assume if *Arvernoceros* and *Rucervus* are synonymous or not, since the shape of antlers is a rather unsafe criterion at the genus level. The definitive conclusion may be obtained from the detailed comparative study of cranial morphology of *Arvernoceros* and *Rucervus*.

According to modern genetic studies, the origin of *Elaphurus davidianus* is related with a hybridization process that took place in Late Pleistocene between *Cervus canadensis* and *Panolia eldi*. Therefore, TEILHARD DE CHARDIN & PIVETEAU's (1930) hypothesis on close relationship between *Elaphurus davidianus* and *Arvernoceros ardei* is not supported. The synonymy between *Arvernoceros* and *Axis* as suggested DI STEFANO & PETRONIO (2000-2002) has a weak support since the Italian authors based their conclusion on a general primitive three-pointed plane of antler construction, which is characteristic of many deer forms that represent early evolutionary stages of all evolutionary lineages. Some antler characters typical for *Arvernoceros* (flattened and branched basal tine, distal part of beam compressed from the sides under the distal ramification) are never recorded in *Axis*.

The radiation of *Arvernoceros*, probably, was caused by temporary geographical isolation of early population with very vast area of distribution across northern part of Eurasia. This fragmentation, probably, was caused by Paratethys transgression in Late Pliocene (VISLOBOKOVA, 1990) that separated Western lineage with *A. ardei* and *A. verestchagini*, and Eastern lineage with *A. ubensis*, *A. bifurcatus*, and *A. giulii*. The evolution of *A. verestchagini* took place, most probably, in the area of the Azov Sea and North Caucasus foothills where numerous remains of *Arvernoceros* of various sizes were recorded (BAIGUSHEVA, 1994). *A. giulii*, probably, is a descent of *A. ubensis* that evolved in the conditions of open woodlands of Asian heartland. *A. giulii* penetrated in Europe somewhat later, by the end of Villafranchian. *Arvernoceros* became extinct in Europe during the End-Villafranchian faunal turnover when climate became colder and more seasonal.

## CONCLUSIONS

Presently, the genus *Arvernoceros* includes five large to very large-sized species with area of distribution from Western Europe to Eastern Asia: *A. ardei* (Early-Late Pliocene, Europe), *A. verestchagini* (Latest Pliocene-Early Pleistocene, Eastern Europe), *A. ubensis* (Late Pliocene, South of Western Siberia), *A. giulii* (Early Pleistocene, Europe), and *A. bifurcatus* (Latest Pliocene-Earliest Pleistocene, China). The genus is characterized by rather conservative specific variability of antler shape and primitive morphology of dentition. *Arvernoceros* belongs to the earliest radiation of Cervinae stock and is phylogenetically very close to, or even synonymous with modern genus *Rucervus*.

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Table. Measurements of the antler of *Arvernoceros ardei* from Slobozia Mare (Moldova) and the neotype of *A. ardei* from Perrier-Etouaires (France).

Tabel. Măsurători ale coarnelor de *Arvernoceros ardei* de la Slobozia Mare (Moldova) și ale neotipului *A. ardei* de la Perrier-Etouaires (Franța).

Measurements	Slobozia Mare	Etouaires (neotype)
Antero-posterior diameter of antler base (mm)	27.3	42.7
Latero-medial diameter of antler base (mm)	28.6	39.0
Height of basal ramification (mm)	71.0	93.0
Maximal diameter of first tine base (mm)	37.5	37.8
Minimal diameter of first tine base (mm)	22.5	26.5
Angle of basal ramification	70°	80°

## FIGURES

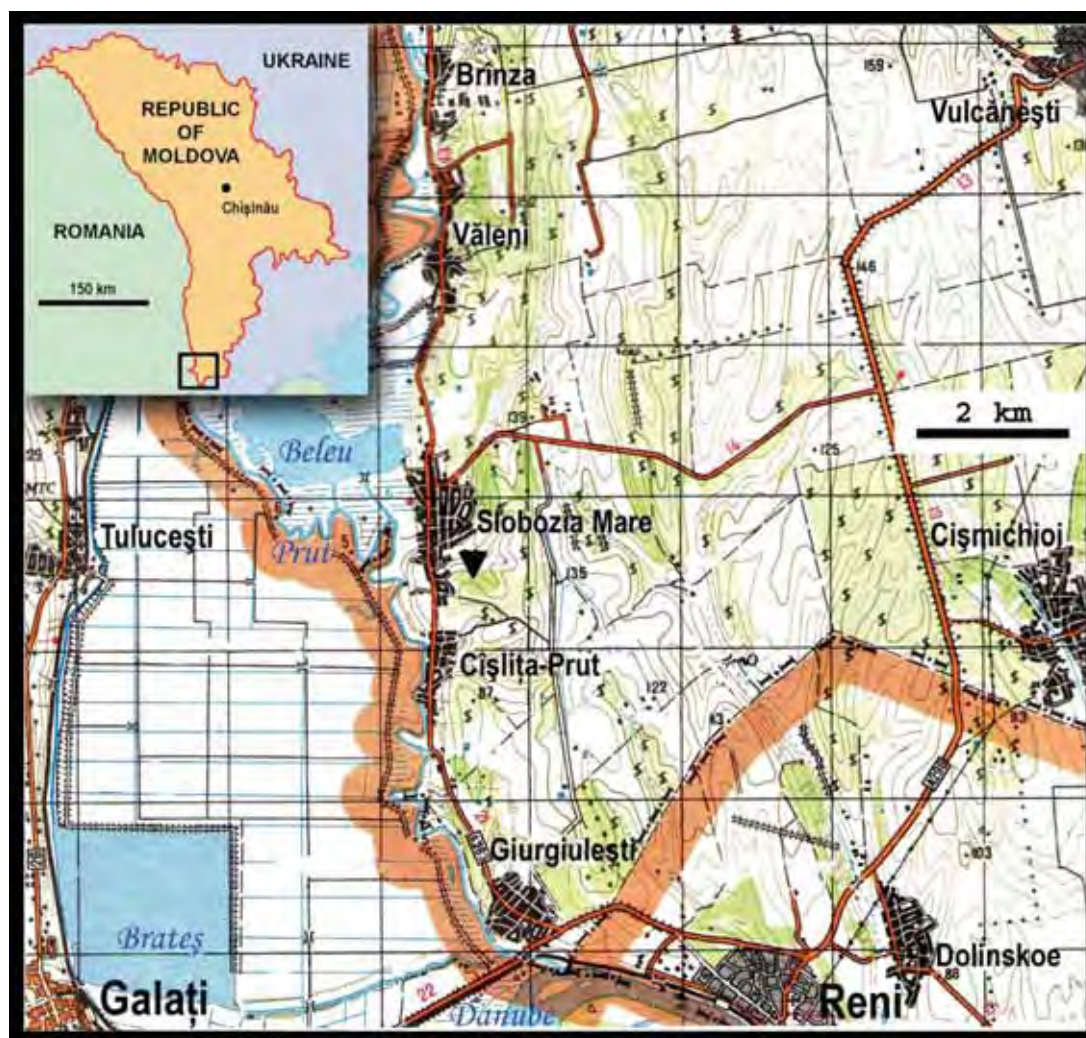


Figure 1. Location map: the black triangle indicates the geographical situation of Rîpa de la Ganu near Slobozia Mare where the fossil material was collected.

Figura 1. Harta. Localizarea Râpei de la Ganu în apropierea satului Slobozia Mare, unde au fost găsite rămășițele fosile, este indicată cu triunghiul negru.



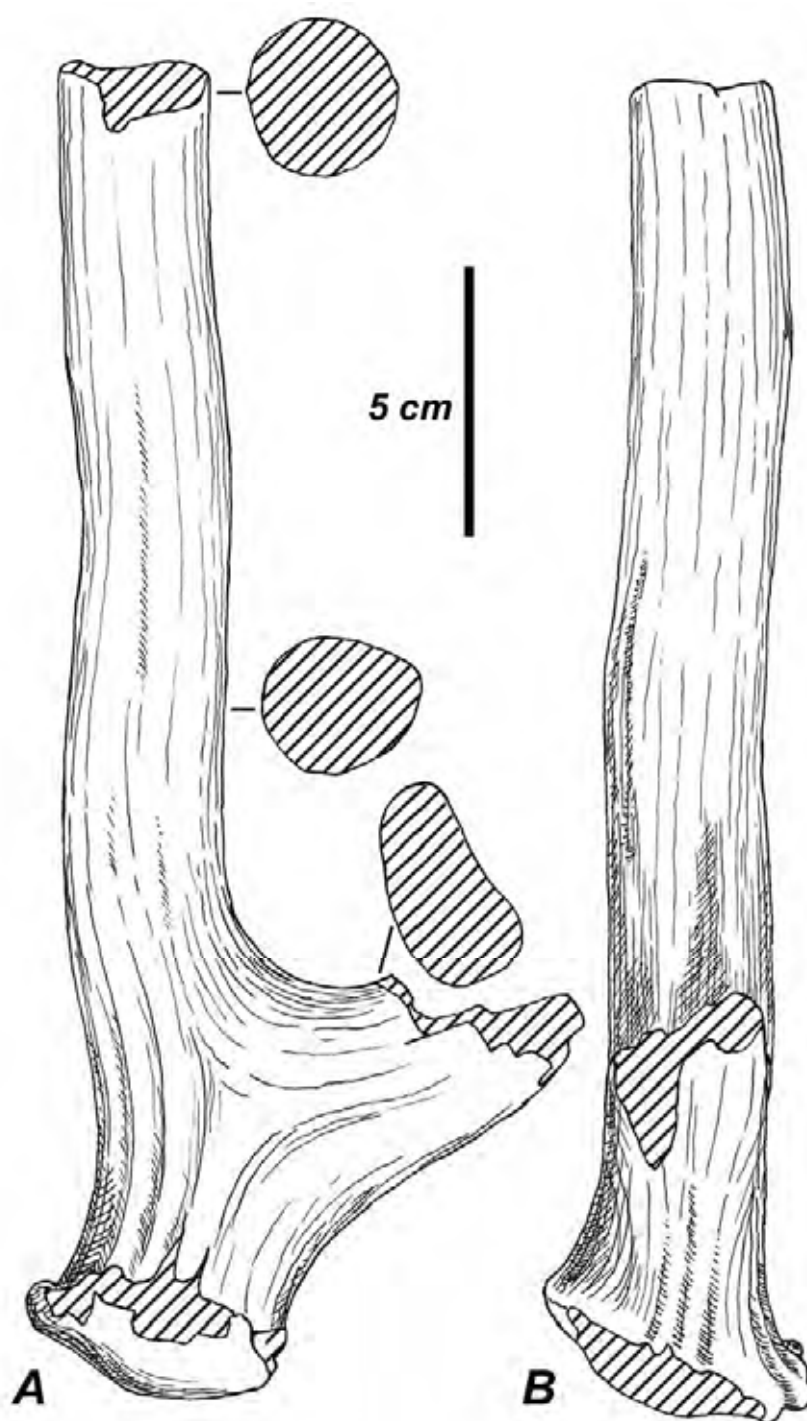


Figure 2. Right shed antler of *Arvernoceros ardei* from Slobozia Mare (Moldova R.): A, lateral view of antler with transverse cross-sections outlines; B, anterior view of the antler.

Figura 2. Corn de cădere drept al *Arvernoceros ardei* de la Slobozia Mare (R. Moldova): A-vedere laterală și secțiunile transversale; B-vedere anterioară.

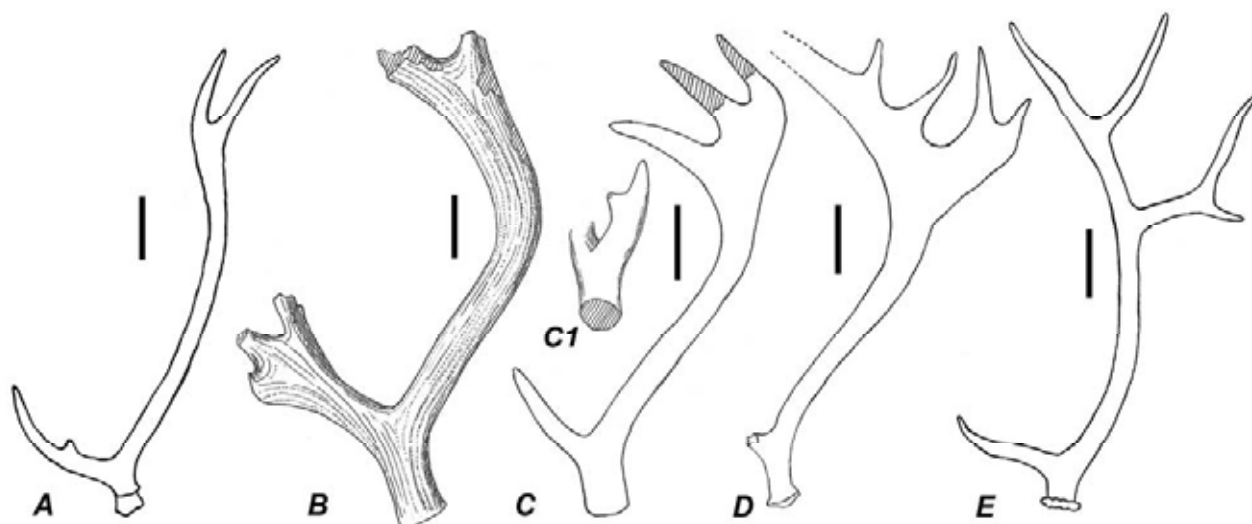


Figure 3. Antler shape of *Arvernoceros* and *Rucervus*: A, *Arvernoceros ubensis*, Altay (adapted from VISLOBOKOVA, 1977); B, *Arvernoceros verestchagini*, Salcia (adapted from DAVID, 1992); C, *Arvernoceros ardei*, Perrier-Etouvaires (neotype); C1, proximal view of basal antler tine of *A. ardei*; *Arvernoceros* from Valea Grăunceanului (reconstruction); *Rucervus duvaucelli*, modern. Scale bar: 10 cm.

Figura 3. Morfologia coarnelor cerbilor *Arvernoceros* și *Rucervus*: A, *Arvernoceros ubensis*, Altay (din VISLOBOKOVA, 1977); B, *Arvernoceros verestchagini*, Salcia (din DAVID, 1992); C, *Arvernoceros ardei*, Perrier-Etouvaires (neotipul); C1, aspectul proximal al razei bazale speciei *A. ardei*; *Arvernoceros* de la Valea Grăunceanului (reconstituire); *Rucervus duvaucelli*, modern. Scara: 10 cm.

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