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On systematic position of “moldavian sambar deer” from the Pliocene of Moldova

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KEY WORDS – Mammalia, Cervidae, Systematics, Morphology, Pliocene, Moldova.

ABSTRACT – The systematic position of the species “*Cervus* (Rusa) moldavicus Janovskaya 1954” is discussed in this paper. The critical revision of the holotype of *Cervus moldavicus* (the so called “moldavian sambar deer”) revealed mistakes in the skull reconstruction that caused a wrong systematic allocation of the discussed species. The skull and dentition morphology suggest that the “moldavian sambar deer” is a fossil roe deer of the genus *Procapreolus*. *C. moldavicus* is considered here as a senior synonym for *Procapreolus wenzensis* (Czyzewska, 1960).

Some ecological and morpho-functional peculiarities of the deer under study, as well as its phylogenetical links, are discussed in the paper.

RIASSUNTO – [Inquadramento sistematico del “sambar della Moldavia” del Pliocene di Moldova] – Nel presente lavoro viene discussa la posizione sistematica della specie “*Cervus* (Rusa) moldavicus Janovskaya 1954”. La revisione dell’olotipo di *Cervus moldavicus* (il cosiddetto “sambar della Moldavia”) rivela alcuni errori nella ricostruzione del cranio, che hanno portato ad una errata collocazione sistematica della specie in discussione. La morfologia del cranio e della dentatura suggerisce che il “sambar della Moldavia” è un capriolo fossile del genere *Procapreolus*. *Cervus moldavicus* viene qui considerato sinonimo senior di *Procapreolus wenzensis* (Czyzewska, 1960).

Vengono inoltre discusse alcune caratteristiche ecologiche e morfofunzionali del cervo in esame ed i suoi legami filogenetici.

INTRODUCTION

The finding of an almost complete skeleton of a young medium-sized female deer from the Pliocene deposits of Bessarabia (the so-called «Bessarabian Roussillion») was mentioned for the first time by I.P. Khomenko (1917). Later N.M. Janovskaya (1954) described this deer under the new species name *Cervus* (Rusa) moldavicus. This author believed that the new species represented a link between the late Miocene representatives of the genus *Cervavitus* and the late Pliocene deer of the genus *Cervus*. However, a careful study of the «moldavian sambar deer» holotype, and also the new discoveries from the Pliocene deposits of Moldova, allow to revise the systematic position of this deer, which we consider similar to the Pliocene roe deer from Weze (Poland).

Family CERVIDAE Gray, 1821
Subfamily ODOCOILEINAE Pocock, 1923
(= NEOCERVINAE Carette, 1922)
Tribe CAPREOLINI Simpson, 1945
Genus PROCAPREOLUS Schlosser, 1924

PROCAPREOLUS MOLDAVICUS (Janovskaya, 1954)

1954 *Cervus* (Rusa) moldavicus n. sp. JANOVSKAYA, pp. 163-164, fig. 1.

1960 *Cervoceros wenzensis* sp. n. CZYZEWSKA, p. 229, pl. 2, fig. 2a, pl. 3.

1968 *Procapreolus wenzensis* (Czyzewska) - CZYZEWSKA, p. 557.

1996 *Procapreolus* sp. PEVZNER, VANGENGIM, VISLOBOKOVA, SOTNIKOVA & TESAKOV, p. 84.

Definition – A rather medium-sized deer, the frontal-orbital part of the skull is shortened, the preorbital pits are larger than in *Capreolus*; intermaxillary bones become evenly narrower in the rostral direction, like in *Capreolus*; the auditory bullae are small and flattened, the acoustic duct is short. The lower jaw has a rather long diastema. The fourth lower premolar (P₄) is characterized by the high fourth degree of molarization, the lower molars have a *Palaeomeryx* fold, the upper ones have protoconal and the hypoconal folds, the cyngulum is reduced. The antlers are three-pointed, thin, lyrated, without bead-like tuberculi at the basis; the first tine is short and located very high.

Holotype – The almost complete skeleton of a juvenile female, Collection of the Palaeontological Institute of the Russian Academy of Sciences (Moscow), No. 2.

Type locality – Fagadil, South Moldova.

1884 *Cervus buladensis* DEPERET, p. 273, pl. VII, fig. 4.

1917 *Cervus* sp. juv. KHOMENKO, p. 61.

MATERIAL

HOLOTYPE

The fragment of braincase (No. 2-1), the forehead fragment (No. 2-2), the left maxilla with the complete tooth row with deciduous premolars (No. 2-3), almost the complete lower jaw with deciduous premolars (No. 2-4), the right femur (No. 2-68), the innominate bones (*dext*, No. 2-67; *sin*, No. 2-65), a diaphysis fragment of the right metatarsal bone (No. 2-71), the left calcaneus (No. 2-70), and the almost complete back bone (tail vertebrae, atlas and epistropheus are absent) and the ribcage.

ADDITIONAL SPECIMENS

The left shed antler with the distal part destroyed (without number, Southern Moldova, Lucești village); an adult individual's left branch of the lower jaw with an almost complete tooth row (P_2 is destroyed; without number, Southern Moldova, Musait village).

DESCRIPTION

HOLOTYPE

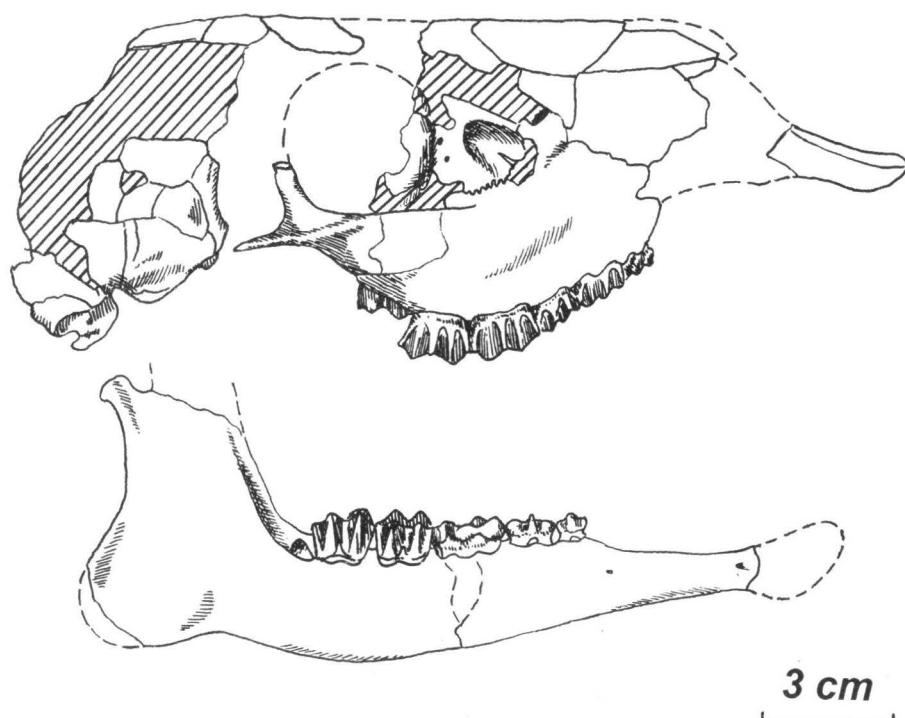
The skull – The careful study of the holotype revealed inaccuracies in the reconstruction of the

skull which obviously have caused the erroneous systematic position of the deer from Fagadil: a) the orbito-frontal part of the skull is artificially lengthened, a fact noticed on joining the parts of the zygomatic arc, placed on the facial and braincase fragments of the skull; b) the angle between the axes of the facial and brain parts is not maintained; c) the axis of the braincase is displaced to the left, the position of the dome bones of the skull is likely to be rather arbitrary too (Text-fig. 1).

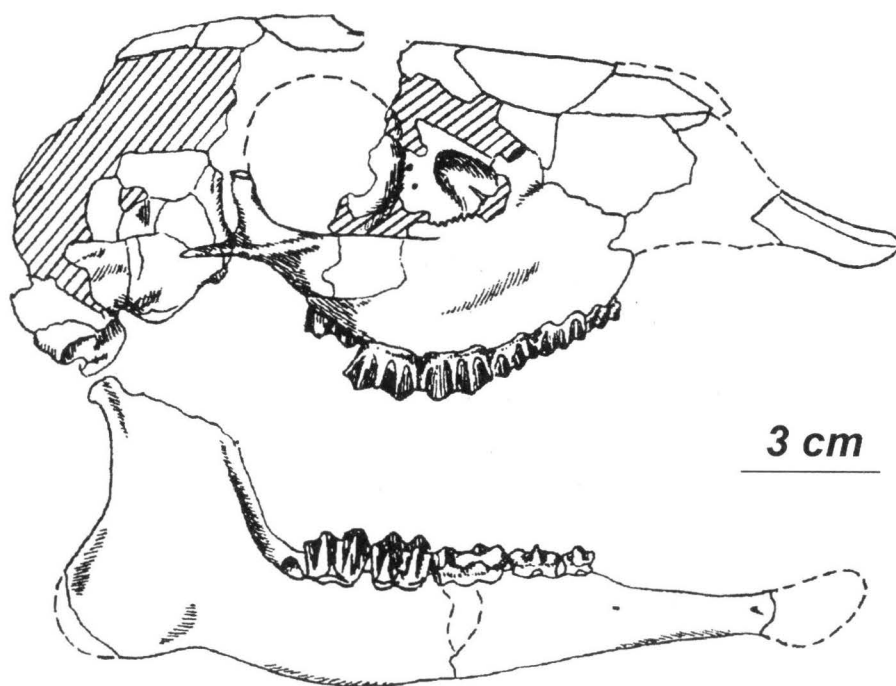
On Text-figures 2 and 3 we tried to reproduce the most probable skull reconstruction, using as a model the fossil craniological material from Weze (Czyżewska, 1968) and recent *Capreolus capreolus* (Flerov, 1952; Sokolov, 1959). The skull of the «Moldavian sambar deer» holotype is rather narrow, a fact already pointed out by N.M. Janovskaya (1954), which could be explained by deformation (Text-fig. 3).

Intermaxillary bones become evenly narrower in rostral direction, like in modern roe deer. The medial side of intermaxillary bears the small incisure characteristic of roe deer. Janovskaya's statement on the presence of the blade-like extension on the antero-external side of intermaxillary bones like in *Cervus* is wrong.

The position of nasalia is very similar to those of the roe deer from Weze (Czyżewska, 1968), its back edge does not reach the line connecting the front edges of the orbits. Back edges of nasalia in *P. mol-*



Text-fig. 1 - The reconstruction of the skull of *Procapreolus moldavicus* (holotype, PIN, No. 2), proposed by N.M. Janovskaya (1954, fig. 1).



Text-fig. 2 - The reconstruction of the holotype skull of *Procaptiveolus moldavicus* with the correct position of the zygomatic arc and the angle between axes of facial and brain parts.

davicus are rounded and do not form an implantation between the frontal bones as in *C. capreolus*.

The praeorbital pits with sharply outlined edges are rather small in *P. moldavicus*, if compared with *Muntiacus*, however, the *P. moldavicus* praeorbital pits are deep and well developed, unlike those of modern roe deer.

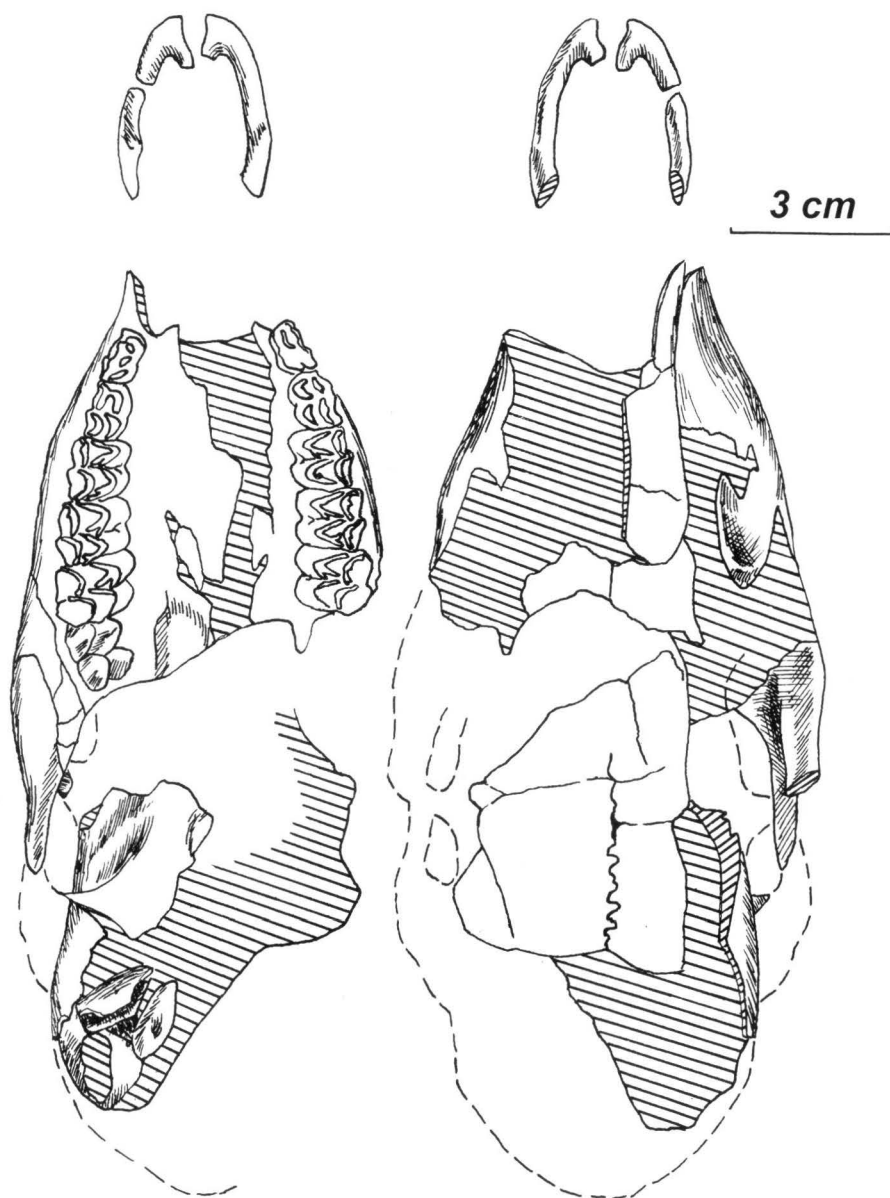
The preserved right acoustic duct is partially destroyed, nevertheless it can be noticed that it is rather short. This speaks for the primitiveness of this character. The acoustic bulla is small, flattened, with

a smooth surface. It is 21.3 mm in length and 13.7 mm in height. The corresponding measurements in *P. moldavicus* from Weze are of 23 mm and 17.8 mm, respectively (Czyzewska, 1968).

Upper molars are characterized by rather high crowns with poorly inclined lingual walls, if compared with other representatives of the genus *Procaptiveolus*. The cingulum is strongly reduced, basal pillars are poorly developed. These characters could be considered as derived. Nevertheless, there are obviously primitive features in the molar morphology: the

Measurements (mm)	<i>P. moldavicus</i> (Musait)	<i>P. cusanus</i> (Lucesti)	<i>P. florovi</i> (Ukraine)	<i>C. capreolus</i> (modern)
1. P ₂ —M ₃ tooth row length	76.8	86.8	68.0-72.5	65.7
2. P ₂ —P ₄ tooth row length	32.0	35.1	28.0-29.0	27.7
3. M ₁ —M ₃ tooth row length	45.3	52.8	39.6-43.5	39.3
4. Mandibular diastema length (foramen mentale—P ₂)	29.4	25.7	40.0	28.5
5. Mandibular corpus depth under P ₂	20.8	18.7		16.7
6. Mandibular corpus depth under M ₁	23.2	23.3		18.1
7. Minimal mandibular diastema depth	13.7	12.4		10.5
Index 2:3	70.6	66.5	65.5-70.7	70.5
Index 6:1	30.2	26.8		27.5
Index 4:1	38.7	29.6	58.8	43.4
Index 2:1	41.7	40.4	39.3-41.1	42.2

Tab. 1 - The sizes and proportions of lower jaw in fossil and modern roe deer (data on *Procaptiveolus florovi* are quoted from Korotkevich, 1974).



Text-fig. 3 - Ventral and dorsal views of the holotype skull of *Procapreolus moldavicus*.

protoconal fold and the spur of hypocone, the wrinkled enamel surface.

The mandible – According to M.N. Janovskaya (1954), the mandible of the sample from Fagadil is characterised by rather wide and low ascending part. The height of the *incisura mandibulae* of the ascending part is 58.5 mm. *Processus angularis* is well developed. The mandible length (approximative) is 174.6 mm. The horizontal mandible ramus is rather high. The mandible height measured between M_1 and pd_4 is 23.0 mm.

The length of the dental series pd_2 — M_2 is 61 mm. Janovskaya (1954) described lower molars as brachiodontous, however, M_1 and M_2 are compara-

tively high crowned. Lower molars are characterised by the weak *Palaeomeryx* fold and ectostylids. pd_4 has a weak *Palaeomeryx* fold, a well developed cingulum and an additional fold at the lingual side (Janovskaya, 1954). pd_2 and pd_3 are three pointed and have no basal structures.

Postcranial skeleton – The lumbar part of backbone is 24.5 cm in length, the thoracic part (approximate, since the third thoracic vertebra is absent) is 35 cm in length. Some hind-limb bones are satisfactorily preserved: unnamed bones, right femur and left calcaneus. The measurements are quoted in table 2. Postcranial bones of the holotype of *Procapreolus moldavicus* will be studied in detail in near future.

Postcranial bones (hip girdle)	Measurements (mm)
<i>Os innominatum (dext)</i> , No. 2-67	
antero-posterior diameter of acetabulum	35.2
transversal diameter of acetabulum	28.6
<i>Os innominatum (sin)</i> , No. 2-65	
antero-posterior diameter of acetabulum	32.5
transversal diameter of acetabulum	27.3
<i>Femur (dext)</i> , No. 2-68	
bone length	230.0
diameter of caput femuri	24.0
length of great trochanter	13.8
width of distal epyphysis	48.7
dorso-ventral measurement of distal epyphysis	59.1
<i>Calcaneus (sin)</i> , No. 2-70	
bone length	78.8
length of tuberosity	53.6
antero-posterior measurement of distal end of tuberosity	18.5
latero-medial measurement of distal end of tuberosity	14.0
<i>Tibia (dext)</i> , No. 2-69	
width of distal epyphysis	30.5
antero-posterior measurement of distal epyphysis	20.3

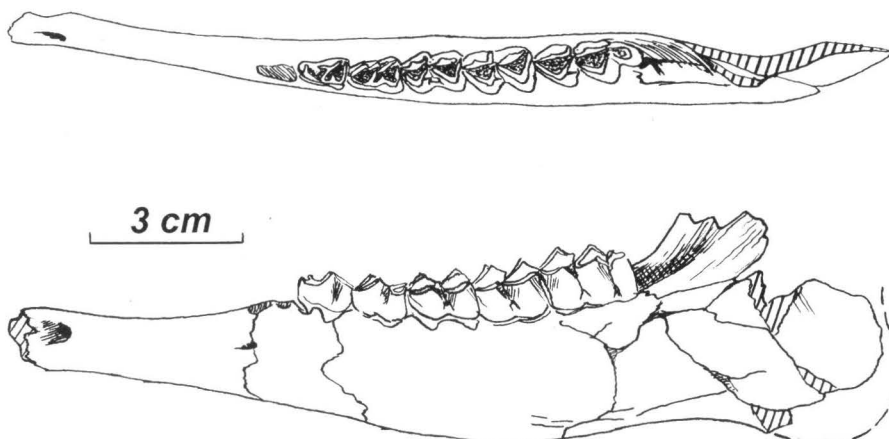
Tab. 2 - Measurements of postcranial bones of *Procapreolus moldavicus* (holotype, the Palaeontological Institute, Moscow).

ADDITIONAL SPECIMENS

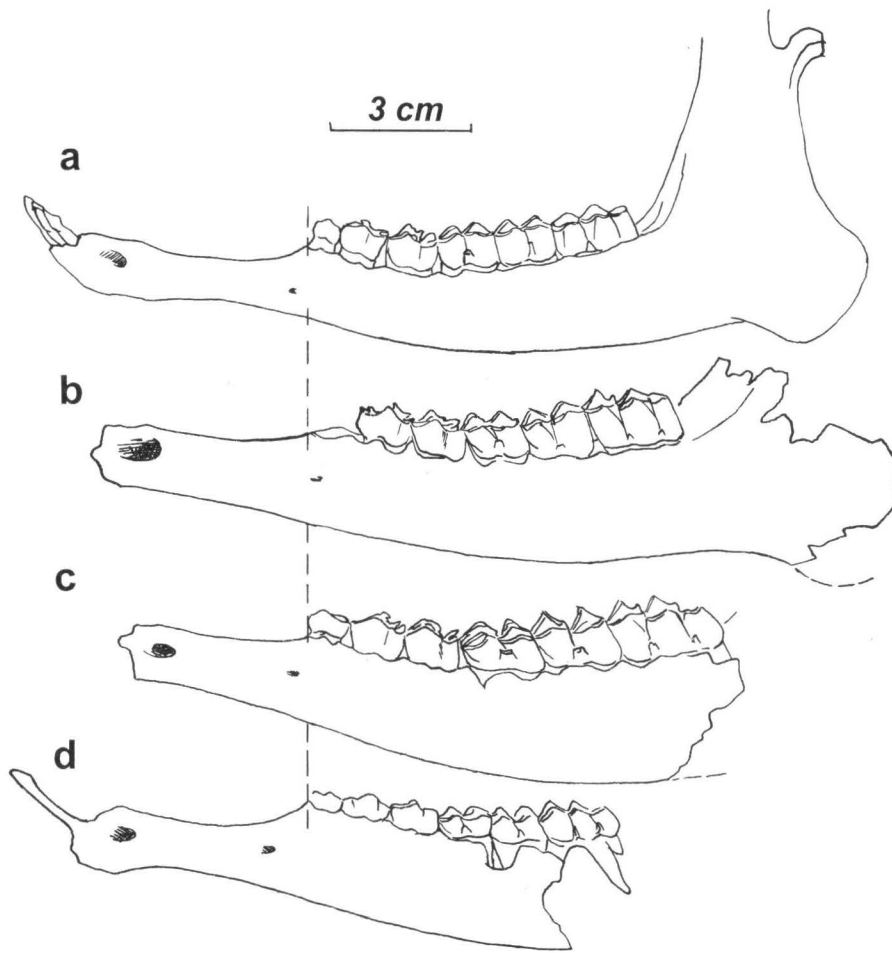
The mandible of *P. moldavicus* from Musait differs by the rather high horizontal branch and the long and strong diastemal portion; processus angularis is well developed. The main measurements and indices of the mandible from Musait (Text-fig. 4) and mandibles of some other fossil and Recent roe deer

are given in table 1. It is necessary to point out that the main mandible proportions of *P. moldavicus* are close to those of *C. capreolus*. The Moldavian fossil roe deer has a longer diastema and a shorter cheek teeth row, a higher and stronger horizontal mandible ramus as compared with *P. cusanus* (Text-fig. 5).

The lower molars have rather high crowns and poorly developed *Palaeomeryx* fold and ectostylids.



Text-fig. 4 - The occlusional and lateral views of the lower jaw of *Procapreolus moldavicus* from Musait (Moldavian assemblage); Department of Paleozoology, Kishinau.



Text-fig. 5 - Mandibles of recent and fossil roe deer: a) *Capreolus capreolus*, b) *Procapreolus moldavicus* (Pliocene, Musait), c) *P. cusanus* (No. 59-3, late Pliocene, Lucesti, Dept. of Paleozoology, Kishinau), d) *P. florovi* (No. 45-3024, Inst. of Zoology, Kiev; late Miocene, South-western Ukraine; adapted from Koro-
tkovich, 1974).

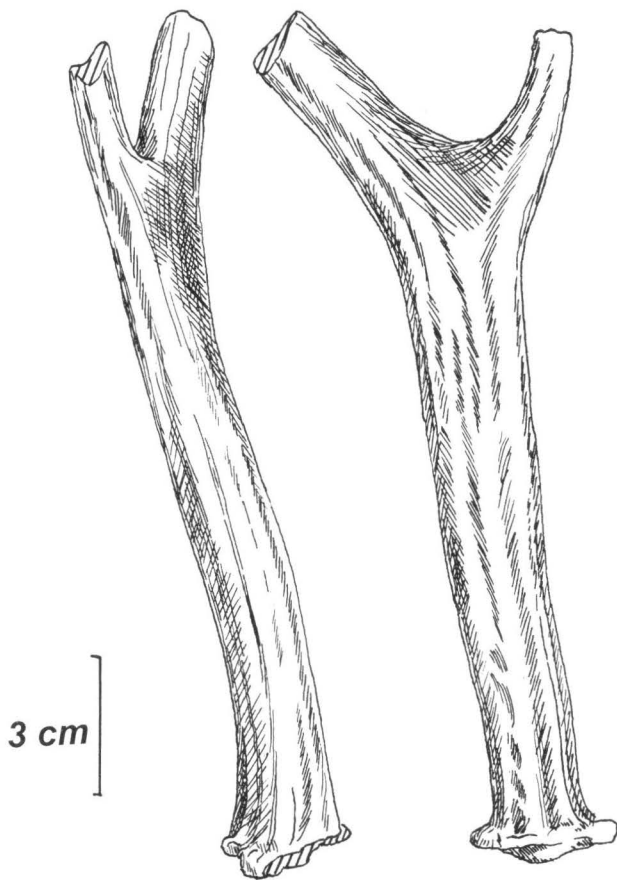
The fourth premolar (P_4) is characterized by the high fourth degree of molarization (according to Heintz, 1970) that is typical for roe deer: the metaconid is strongly extended forward and fused with the paraconid, it closes the anterior valley; the paraconid is not supplemented by the parastilid. The entoconid is well developed, its junction with the hypoconid is interrupted. The anterior end of the entoconid merges with the metaconid, the posterior part of the entoconid approaches to the entostilid, limiting the posterior valley.

In the third premolar, the paraconid is supplemented by the parastilid; the metaconid is deflected backward being slightly extended antero-posteriorly. The entoconid is not connected with the hypoconid (most likely, because of the weak tooth wear), it merges with the metaconid forming a single structure.

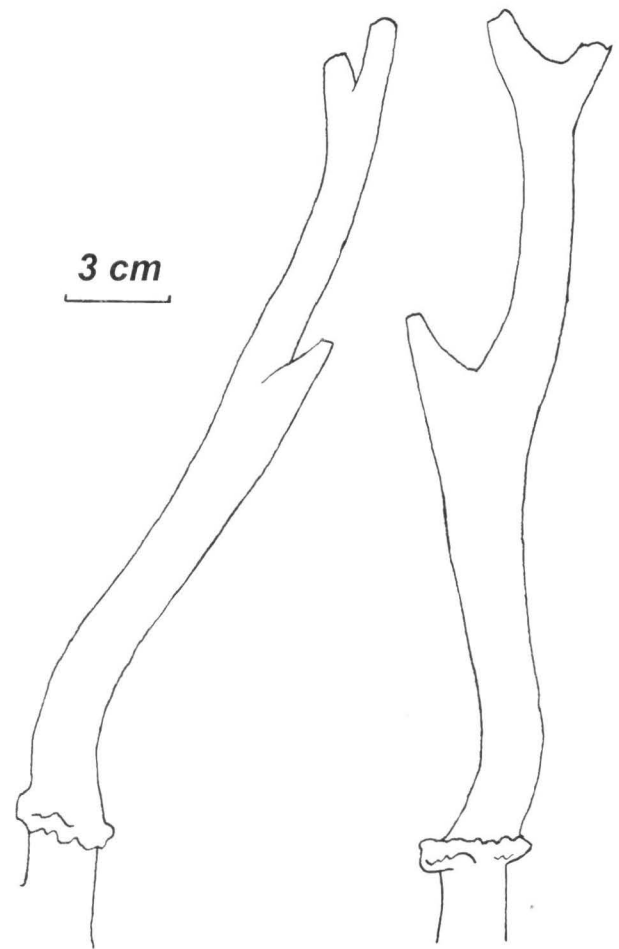
The antler from Lucesti (Text-fig. 6) is characterized by a slender beam and very high location of the first tine. The transverse section of the beam above the burr is almost circular. Right above the burr the antler beam deflects laterally, gradually flattening lat-

tero-medially towards the first ramification. The first tine is short and forms a ramification angle of about 70° . The antler surface is smooth without tubercles. The height of the first ramification is 165.7 mm, the antero-posterior diameter of antler base is 24.3 mm, the latero-medial one is 24.0 mm. Unlike the antlered skull No. 220 from Weze, Poland (Czyzewska, 1960) (Text-fig. 7), the antler from Lucesti is not marked by a S-like bending at the antler base. I am inclined to think that this character has no systematical value. It could be referred to individual variability that is rather common in the antler morphology. The morphology of the antler from Lucesti is very close to that of *Cervus buladensis* from France (Deperet, 1884) characterized by a slim and strait basal antler portion and a high insertion of the first tine (15 cm above the burr).

The basal fragment of the antler from Malusteni (Romania), characterised by a very high insertion of the first tine on the slender beam and described by I. Simionescu (1977, p.453, fig. 58) as *Cervus buladensis*, also seems to be very close to the specimen from Lucesti.



Text-fig. 6 - The antler of *Procapreolus moldavicus* from Lucesti (Pliocene, Moldavian assemblage), frontal and lateral views (Dept. of Paleozoology, Kishinau).



Text-fig. 7 - The antler of *Procapreolus moldavicus* from Weze (No. 220, Pliocene, Poland) (adapted from Czyżewska, 1968).

Note – Deperet (1884, p. 273, pl. VII, fig. 4) described fossil remains of a small-sized deer from Perrier and Etouaires (France) as *Cervus buladensis*. Slim and slightly flattened antlers, which characterize this species, have a first short tine inserted very high above the burr. Morphology and some measurements quoted by Deperet (1884) seem to be very close to those of the samples from Moldova.

The Deperet's ancient roe deer described as *Cervus buladensis* undoubtedly is very close to the «Moldavian sambar deer». However, this species name could be considered as *nomen oblitum*, as it was not used for a period longer than 50 years, since Simionescu (1930, reedited in 1974) mentioned this species name describing the Pliocene fauna from Malusteni (Romania). The material described by Deperet (several postcranial bones and a fragment of antlered skull) was never mentioned later. I am not sure if it is reasonable to replace the well-known species name *moldavicus* by *buladensis nomen oblitum*.

SOME REMARKS ON FUNCTIONAL MORPHOLOGY OF *PROCAPREOLUS MOLDAVICUS*

LOCOMOTION

The satisfactory preservation of the backbone and femur in the Fagadil sample is of special interest, as it allows to reconstruct the locomotion strategy and the probable habitat of the fossil deer. The length ratio index of the femur and thoraco-lumbar portion of the backbone in *Procapreolus moldavicus* and some Recent species of deer and bovids are compared in table 3. The majority of modern deer are woodland and forest inhabitants. They are characterized by adaptations to the saltatorial locomotion, such as the lengthened femur, the shortened thoraco-lumbar portion of the backbone, the strong calcaneum, etc. (Sokolov *et al.*, 1964; Gambarian, 1972; Sutula, 1990). Such a proportion of the main segments of the

skeleton provides a more caudal position of the gravity centre (C.G.) of the animal body that increases the vertical component of the propulsive thrust of hindlimbs. Bovids and tundra reindeer, inhabiting open landscapes, don't have the necessity to overcome different obstacles, like bushes, etc. The following adaptations to the cursorial locomotion could be noted in those animals: the shortening of femur and the elongated thoraco-lumbar part of the backbone. The shortened limbs and the elongated axle body cause the offset of the C.G. cranially and tend to increase the horizontal component of the propulsive thrust transmitted to the body by the hindlimbs (Sutula, 1990). We can see (table 3) that the value of the femur/backbone ratio of *Procapreolus moldavicus* is closer to those of modern deer, and in particular, to the value of the index of Recent roe deer. It suggests that *P. moldavicus* possesses the same postcranial skeleton morphology as the Recent saltatorial runners.

DIET ADAPTATION

The shape of the craniomandibular articulation could provide us with information on the diet adaptation of the fossil animal. The preserved right articulation surface of the lower jaw of the Fagadil holotype has an oval symmetric form and lies in a horizontal plane (Text-fig. 8a). In *Muntiacus* (Text-fig. 8b), which feeds on more juicy and softer forage, the articulation surface of the lower jaw is inclined medially and has a triangular shape, and its postero-medial parts form an oblique backward plane. In modern roe deer (Text-fig. 8c) the articulation surface morphology has an intermediate character: it is slightly asymmetric and its postero-medial segment is placed in oblique backward planes, though the general shape of the articulation surface is close to oval and its main part lies in a horizontal plane.

From the characters described above, it is possible to conclude that the strong mandibles with deep cor-

pus and long diastema on one hand, and the symmetric and horizontal articulation surface ensuring the possibility of side movements of the jaw on the other hand, are an adaptation to repeated mastication of coarse food (Spenser, 1995, 1997; Vizcaino & Fariña, 1997). As stressed above, *P. moldavicus* is characterised by unusually high molar crowns that confirm our conclusion. As Janovskaya (1954) correctly noticed, this deer lived under rather dry conditions in half-open spaces, its dietary preferences included rough grassy forages, unlike the modern roe deer, which eat rather soft dicotyledon and tree shoot forage (Sokolov, 1959).

The functional morphology of postcranial bones, dentition and mandible suggests that *P. moldavicus* inhabited the dry subtropical landscapes mosaically composed of woodland and savanna. The flora of the early stage of the Moldavian assemblage was likely to have represented a combination of high grassy vegetation and arboreous plants.

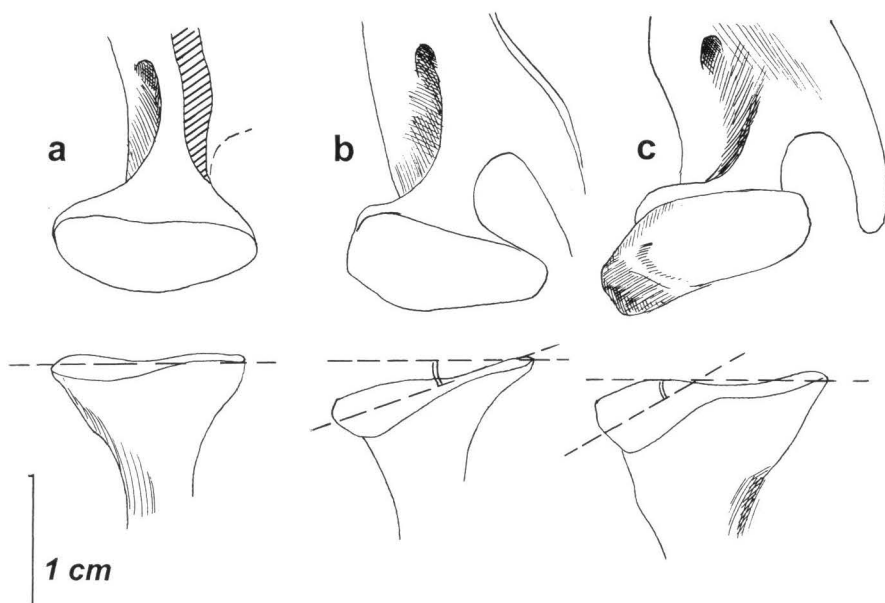
PHYLOGENETICAL RELATIONSHIPS

P. moldavicus undoubtedly belongs to the phylogenetical stock that also includes the late Miocene *P. ucrainicus* and *P. florovi* from Ukraine and Recent roe deer (Vislobokova & Kalmykov, 1994). *P. moldavicus* shares with *P. florovi* the high insertion of the first tine, the short cheek tooth row, the presence of the *Palaeomeryx* fold and the reduced cingulum. I. Vislobokova and N. Kalmykov (1994) consider *Procapreolus moldavicus* to be a descendant of *P. florovi* and the most probable ancestor of modern roe deer. During this evolution stage roe deer lost the *Palaeomeryx* fold, the *fossa preorbitalis* became small, the mandible became more slender, the first ramification shifted towards the burr.

E.L. Korotkevich and N.G. Belan's (1986) point of view on the phyletical link between *P. moldavicus* and *P. cusanus* is not acceptable. These deers are a

Species	TLP (cm)	F (cm)	F/TLP
<i>Procapreolus moldavicus</i>	59.5	23.0	38.7
<i>Dama dama</i>	59.5	19.6	37.9
<i>Cervus nippon</i>	59.5	21.7	36.4
<i>Cervus elaphus</i>	73.7	22.2	38.3
<i>Capreolus capreolus</i>	50.0	28.3	39.2
<i>Rangifer tarandus</i> (woodland form)	74.3	30.8	40.4
<i>Rangifer tarandus</i> (tundra form)	74.1	25.5	34.5
<i>Gazella gutturosa</i>	50.2	17.8	35.4
<i>Saiga tatarica</i>	50.7	17.2	33.9

Tab. 3 - Relative and absolute sizes of the thoraco-lumbar portion of backbone (TLP) and femur (F) of *Procapreolus moldavicus* and some recent species of deer and bovids (according Sutula, 1990).



Text-fig. 8 - The shape of mandible articulation surfaces of *Procapreolus moldavicus* (a) (PIN, No. 2-4), *Muntiacus muntjak* (b), *Capreolus capreolus* (c).

good example of parallel evolution of two related species that achieved diametrically opposite evolutionary specializations. Unlike *P. moldavicus*, *P. cusanus* has flattened antlers with the comparatively low situated first tine, the cheek tooth row is comparatively and absolutely longer, while the diastema is very short. Upper premolars in *P. cusanus* maintain the highly folded enamel that is considered here as a primitive character, while lower molars lack the *Palaeomeryx* fold. *P. cusanus* dentition is characterised by brachiodont cheek teeth with strongly inclined lingual surfaces, unlike that of *P. moldavicus*. We can see that the dentition morphology of the Pliocene roe deer displays the completely different mosaical combination of primitive and advanced characters, a fact that rules out the direct phyletical link between them.

Note – The fossil remains of the medium-sized deer from Etulia (Moldova) described by L.I. Alexeeva (1977) as *Cervus (Rusa) moldavicus*, belong to a different species of the Cervinae group. The fragments of maxillae (GIN, No. 428-225, No. 428) should be referred to the genus *Pseudodama* (Azzaroli, 1992) which contains the European medium-sized deer of the *Axis* type. Namely, the measurements of the upper molars surpass approximately by one third those of the deer described by N.M. Janovskaya and the characteristic protoconal enamel fold is lacking. The fragments of antlers (GIN, No. 428-218, No. 428-230) belong to a rather large deer that seems to be close to *Cervus perrieri* (Vislobokova, personal communication).

Distribution – Early-late Pliocene, the Moldavian assemblage, Moldova, Poland, Romania, France.

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