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Roman Croitor. Genus Bison (Bovidae, mammalia) in Early Pleistocene of Moldova. Materialele conferinței naționale cu participarea internațională "Mediul și dezvoltarea durabilă", Ediția a III-a / 3rd National Scientific Conference with international participation "Environment and sustainable development", Oct 2016, Chisinau, Moldova. hal-01766112

HAL Id: hal-01766112

<https://hal.science/hal-01766112>

Submitted on 13 Apr 2018

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GENUS *BISON* (BOVIDAE, MAMMALIA) IN EARLY PLEISTOCENE OF MOLDOVA

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Abstract. Remains of *Bison* (*Eobison*) sp. from Salcia and Ursoaia, and *Bison* cf. *menneri* from Cișmichioi-III and Hadjimus are briefly described and discussed. The paper also proposes an overview of most important Early Pleistocene bison findings from Eastern and Southern Europe and a discussion of their taxonomy and paleobiogeography.

Keywords: Early Pleistocene, Southeastern Europe, *Bison*, taxonomy, paleobiogeography.

INTRODUCTION

The genus *Bison* is an important element of Pleistocene faunas of Moldova and adjacent regions occupying a specific ecological niche of a largest ruminant herbivore in boreal paleoecosystems. Despite of several studies on archaic *Bison* carried out for more than half a century, the discussions on unresolved taxonomic, systematic, paleoecological, and biogeographic questions are still open [1, 4, 5, 8, 10, 11, 13, 14, 15, 16, 18]. The unresolved taxonomical issues are mostly caused by the incomplete fossil record that makes impossible the comparison of described species and samples. The knowledge gaps in taxonomy and evolution of early *Bison* impede biogeographic and paleoecological study of this systematic group. The present communication proposes an overview of archaic fossil bison forms from Moldova and adjacent areas, as well as an attempt to clarify the paleobiogeography of *Bison* in Early Pleistocene of Western Eurasia.

MATERIAL AND METHODS

The studied material is stored in the Institute of Zoology (IZ) of the Academy of Sciences of Moldova and in the Moldavian Hydrogeological Expedition (MHE). The standard osteological measurements [4, 13, 14, 16] are applied in the study. The fossil comparative material involved in the present study comes from the following institutions: Apollonia-1 (University of Thessaloniki, Greece); Pirro Nord, Capena (University of Florence, Italy); Semibalki (Azov Museum of Local Lore, Russia). The following biometric data are adapted from bibliographic sources: Untermassfeld [16]; Dmanisi [4]; Cherevichnyi, Chortkiv, Kairy [9]; Tzimbal [18]. The abbreviations used in the text: DAP, anteroposterior diameter; DDV, dorsoventral diameter; DLM, lateromedial diameter; L, length; D, breadth; GIN, Geological Institute, Moscow; PIN, Paleontological Institute, Moscow; IZU, Institute of Zoology, Kiev.

Systematic description

Family Bovidae Gray, 1821

Subfamily Bovinae Gill, 1872

Tribe Bovini Simpson, 1945

Genus *Bison* H. Smith, 1827

Subgenus *Eobison* Flerov, 1972

Bison (*Eobison*) sp.

A limited number of remains of a small-sized primitive bison comes from Salcia (Southeast Moldova): a talus (no number, IZ: ♀?, [8]: tab. 4), two metacarpal bones (no numbers, IZ: ♀, L max - 235.0 mm; ♂, L max - 254.0; [8]: tab. 3), three proximal fragments of radius (Nrs. 52-332, 52-1162, 52-341, IZ; [8]: tab. 2). A second anterior phalanx of *Bison* (*Eobison*) sp. comes from Ursoaia (no

number, MHE, ♂, [8]; Fig. 1). Measurements of the talus from Salcia approach the specimen under study to the material from Apollonia-1, Capena, and Dmanisi (Fig. 2-C). Measurements of proximal epiphyses of radius from Salcia, Apollonia-1, and Dmanisi show a great dispersal, apparently, due to a strongly expressed sexual dimorphism (Fig. 2-B): the sample from Salcia is grouped with the smaller specimen from Apollonia (females?), while the sample from Dmanisi is grouped with the larger specimen from Apollonia and the specimen from Capena (males?). With exception of talus bones, the studied skeletal material does not overlap on the scattered diagrams with *Bison menneri* from the Epi-Villafranchian of Untermassfeld (Germany). The metacarpals from Salcia are comparatively robust and form on the diagram (Fig. 2-A) a dense cluster with samples from Apollonia-1, Capena, Dmanisi, as well as with the specimen from Cherevichnyi (South Ukraine). The second phalanx from Ursoaia is very robust and much shorter than the sample of *B. menneri* (Fig. 2-D). The most plausible explanation is that the phalanx from Ursoaia belongs to a male bison similar to *B. (Eobison) sp.* from Apollonia-1.

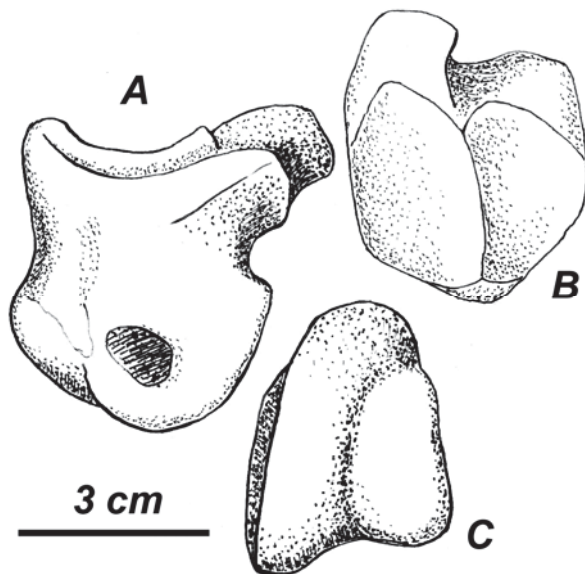


Figure 1. The second anterior phalanx of *Bison (Eobison) sp.* from Ursoaia, Moldova (no number, MHE, ♂): A, medial view; B, proximal view; C, distal view.

The species determination of the majority of findings of primitive Early Pleistocene bison from Southeastern and Southern Europe is difficult due to the incomplete paleontological record and insufficient knowledge of already described species. The type of *B. (Eobison) tamanensis* is a poor left occipital fragment with a basal part of horn core (Nr. 26010/1, ZIN) from the post-Villafranchian fauna of Tzimbali (Taman Peninsula, Russia) that together with another horn core fragment was originally reported by Verestchagin [18] as *Bison sp.* The species name “*Bison sp. (tamanensis N. Ver.)*” [sic] proposed by Verestchagin [19] did not correspond to the requirements of ICZN, since the new species name was not accompanied with diagnosis, description, type designation, and a clear reference to figure of type specimen. The species name *Bison tamanensis* Verestchagin 1959 was validated later by Flerov [10], who proposed a diagnosis and designated the cranial fragment Nr. 26010/1 (ZIN) as a holotype (actually, this is a lectotype), and a reference to the figure of type specimen published in Verestchagin [19]. According to Flerov [11], *B. (Eobison) tamanensis* shares with *B. (Eobison) palaeosinensis* from Nihowan large and deep temporal fossae, however, it differs from the latter species by the broader skull constriction behind horn-cores. The horn core of Tamanian bison is somewhat compressed dorsoventrally (DAP×DDV: 95.0×75.0 mm), while the estimated length of horn-core amounts to 210-260 mm [18].

Baigusheva [3] reported a partially preserved skull of *Bison cf. tamanensis* from the layer 4-5 of Semibalki (Taman Peninsula). The bison from Semibalki (stored in the Azov Museum) is characterized by flattened frontal bones, very long and broad nasal bones (L=240.0 mm, dx; D=70.0 mm, sin), well-

expressed post-cornual constriction, compressed dorso-ventrally (more than in the type specimen of *B. tamanensis*) horn cores (DAP×DDV: 105.1×69.0 mm). The distal portion of horn-core is sharply curved, so its tip is set in vertical position. Other available measurements: D occipital: ca. 270 mm; D occipital condyles: 199.2 mm; L nasion – opisthocranium: 275.0 mm.

Kostopoulos [13] described *B. (Eobison) sp.* in the composition of late Early Pleistocene fauna from Apollonia-1 (Greece). The fossil material is represented by postcranial bones, upper and lower jaw fragments, while diagnostic cranial material and horn cores are missing. Kostopoulos [13] noticed the intermediate character between *Leptobos* and *Bison priscus* proportions of metacarpals and the measurements of dentition standing close to *B. (Eobison) palaeosinensis*. I would like to indicate also the strong sexual dimorphism in postcranial measurements and proportions of the bison from Apollonia-1 that should be taken in account in comparative studies.

Bukhsianidze [4] included in *B. (Eobison)* the Late Villafranchian species *Dmanisibos georgicus* Burchak-Abramovich & Vekua, 1994 from Dmanisi (Georgia). The holotype of *B. (Eobison) georgicus* is a horned skull destroyed before orbits. According to Bukhsianidze [4], the Georgian species shares with primitive *Bison* the large and deep temporal fossae, the typical postcornual constriction, and the shape and position of horn cores. The holotype of *B. (Eobison) georgicus* has similar to *B. (Eobison) tamanensis* diameters of horn-core base (DAP×DDV: 92.1×73.6 mm), but its horn cores seems to be much longer (ca. 344 mm *vide* [5]). Despite of long horn cores, the available cranial measurements (L nasion – opisthocranium: 233.0 mm; D occipital condyles: 99.8 mm) are slightly inferior to those of the cranium from Semibalki. The postcranial measurements of Georgian *Eobison* are similar to those of the samples of Salcia, Apollonia, and Capena (Fig. 2-A, B, C).

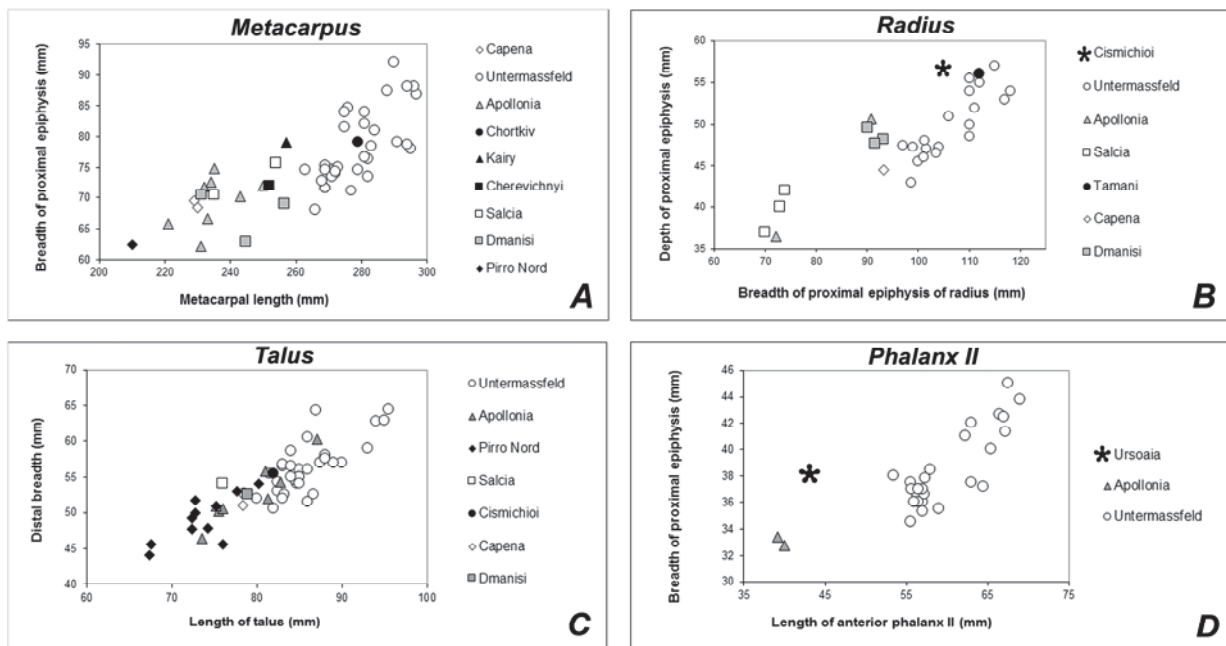


Figure 2. Comparison of measurements of postcranial bones of Early Pleistocene archaic representatives of the genus *Bison* from Western Eurasia. The measurements of *Bison* samples and specimens are adapted from the following authors: *Bison menneri* (Untermassfeld) [16]; *B. menneri* (Tzimbali) [18]; *B. menneri* (Chortkiv) [9]; *B. cf. menneri* (Çișmichioi) [8]; *Bison (Eobison) sp.* (Apollonia) [8, 13]; *B. (Eobison) sp.* (Capena) [8, 14]; *B. (Eobison) sp.* (Salcia) [8]; *B. (Eobison) sp.* (Ursoaia) [8]; *B. (Eobison) sp.* (Cherevichnyi) [9]; *B. (Eobison) sp.* (Kairy) [9]; *B. (Eobison) georgicus* (Dmanisi) [4, 5]; *B. (Eobison) degiulii* (Pirro Nord) [8, 14].

Bison sukhovi Alekseeva, 1967 from Dolinskoe (Odessa Region, Ukraine) is based on a comparatively small and little curved horn core (Nr. 391-2, GIN) with sub-triangular shape of cross-section that reminds *B. (Eobison) sivalensis* and cranium “B” from Nihowan regarded by Teilhard de Chardin and Piveteau [17] as a female of *Bison (Eobison) palaeosinensis*. Basal diameters of the horn core from Dolinskoe (DAP×DDV: 72.0×62.0 mm: [2]) stand closer to the analogous measurements of a presumed young female of *B. (Eobison) georgicus* from Dmanisi (56.7×55.2 mm: [4]). Most probably, the horn core from Dolinskoe belongs to a female and, therefore, *B. sukhovi* is a synonym of *B. (Eobison) tamanensis* [8]. A small, but relatively robust and weakly curved horn core similar to the “*sukhovi*” type was discovered in the “early Tamanian age” site Kairy (Kherson Region, South Ukraine) in association with rather robust metacarpus [9], which is shorter than metacarpals from Untermassfeld and stands close to the largest specimen from Salcia (Fig. 2-A).

A small-sized bison *Bison (Eobison) degiulii* with rather restricted distribution in Southern Italy (its remains are known only from Pirro Nord; bison remains from other fossiliferous sites ascribed to this species are questionable) also represented a taxonomical difficulty. The species name *Bison (Eobison) degiulii* was proposed for the first time by Masini [14] in his doctoral thesis and this taxonomic act did not fulfil the requirements of ICZN for species description and publication. Nonetheless, it seems that the species name *B. (Eobison) degiulii* Masini, 1989 was validated later by Masini et al. [15]: although the paragraph dedicated to this species is not clearly structured, it contains an indication of holotype, the figures of the holotype (fig. 9 in [15]), an indication of type locality, a completed diagnosis (therefore, the cited authors act as first reviewers of the species), and a geological distribution.

B. (Eobison) degiulii Masini, 1989 from the final stage of Early Pleistocene of Pirro Nord (Italy) has the most detached position among primitive *Bison* of Europe [14]. It is somewhat smaller than *Bison* from Capena, Apollonia-1, Salcia, and Dmanisi and approaches to the body size of *Leptobos*. The type specimen (a partial skull with destroyed horn cores) from Pirro Nord is distinguished from *B. (Eobison) georgicus* and *B. cf. tamanensis* from Semibalki by remarkably convex pneumatized frontal bones, smaller and narrower temporal fossae and less expressed postcornual constriction [4, 14, 15]. Masini et al. [15] referred with a certain caution a horn core from Mugello Basin (Italy) to *B. (Eobison) degiulii*. It is characterized by a dorso-ventral compression and a marked curve in upper direction in its distal portion. Apart from its smaller size, the horn core from Mugello Basin reminds *B. schoetensacki* [15]. According to Bukhsianidze [4], *B. degiulii* belongs to the subgenus *Bison (Bison)*, since its specialized cranial morphology is closer to the advanced type of bison.

Subgenus *Bison* H. Smith 1827

Bison cf. menneri Sher, 1997

Few remains of a larger bison from Early Pleistocene of Moldova show affinity with *B. menneri* from Epi-Villafranchian of Untermassfeld (Germany): a distal fragment of humerus from Hadjimus (“Hadjimus-71”, IZ), and a proximal fragment of radiocubitus from Cișmichioi-III (Nr. 19/2461, IZ). The measurements of proximal epiphysis of radius from Cișmichioi-III (DLM = 105.3 mm; DAP = 56.6 mm) are close to the dimensions of males of *B. menneri* (Fig. 2-B).

Bison remains that show affinity to the sample from Untermassfeld are less common in Eastern Europe, therefore, they worth mentioning. The metacarpus Nr. 30-275 (IZU) from Chortkiv (Ternopil Region, Western Ukraine) is remarkably long and thin [9] and falls within the variation range of *B. menneri* (Fig. 2-A).

The left radius Nr. 26009/4 (ZIN) from Tzimbai (Taman Peninsula) described by Verestchagin [18] as *B. cf. schoetensacki* fits perfectly with the dimensions of the sample from Untermassfeld (the measurements of the specimen from Tzimbai according to Verestchagin [18] are the following: L = 372.0 mm; DLM prox. = 112.0 mm; DAP prox. = 56.0 mm). *B. menneri* from Untermassfeld is characterized by exceptionally elongated and slender radius proportions among Quaternary bovids [16],

therefore, there are no doubts that the radius from Tzimbal belongs to *B. menneri*. A robust (base circumference amounts to 260 mm) and quite short (estimated L ca. 345 mm) right horn core Nr. 26009/4 (ZIN) from Tzimbal with a circular cross-section was also ascribed to *B. cf. schoetensacki* [18]. There is a high probability that this specimen from Tamanian fauna also belongs to *B. menneri*. The species *B. menneri* is based on a rich postcranial material, mandibles and dentitions from the Epi-Villafranchian fauna of Untermassfeld [16]. The main taxonomical difficulty in the case of the bison from Untermassfeld is caused by missing adult cranial material that makes problematic the comparison of *B. menneri* with other archaic bison species described on the basis of cranial material. Poor cranial remains of juvenile individuals permitted to Sher [16] to report the following primitive cranial characters approaching *B. menneri* to *Eobison*: the gently concave frontals between horn cores, the convex sagittal profile of skull roof, the broad temporal fossae, and the directed somewhat backward horn cores.

DISCUSSION AND CONCLUSIONS

The Early Pleistocene bison remains from Moldova belong to two distinct forms: a somewhat smaller and rather archaic form from Ursoaia and Salcia (IXth terrace of Dniester) with short metapodials similar to *B. (Eobison) sp.* from Apollonia-1, Dmanisi, Cherevichnyi, Kairy, and Capena, and a larger bison from Cișmichioi (VIIth terrace of Prut: [12]) and Hadjimus (VIIIth terrace of Dniester: [12]) that is close to *B. menneri* from Untermassfeld. It is noteworthy that, besides *B. cf. menneri*, the fauna from Cișmichioi also contains a large-sized deer *Arvernoceros sp.* similar to *A. giulii* (= *Eucladoceros giulii* Kahlke, 1997) from the Epi-Villafranchian fauna of Untermassfeld [7]. Both large-sized ruminants are the specific elements of the fauna from Untermassfeld and permit to find a more exact biostratigraphic position of the faunas from Cișmichioi. It seems that the identified primitive forms of *Bison* from Moldova were not contemporaneous.

The dispersal of primitive *B. (Eobison)* ranged in the southern latitudes of Eurasia from China to Western Europe [10, 11, 16, 17]. The chronology of first occurrence of *Eobison* in Western Eurasia is unclear. Bukhsianidze [4] traced the lineage of *Bison* in Europe from Late Pliocene “*Leptobos*” *stenometopon* through “*Leptobos*” *elatus*. The latter species was also included in *B. (Eobison)* [4], however, this viewpoint was not supported [15]. Remains of *Eobison* became more frequent in Early Pleistocene of Caucasus, Southeastern Europe, Balkans, and Italian peninsula. Actually, *B. (Eobison)* is a specific faunal element shared by Southern Asia and Southeastern Europe suggesting faunal dispersals between those two biogeographic areas. Apparently, *Eobison* got extinct earlier in Southern Asia, but survived in Southern Europe until early Middle Pleistocene and possibly even evolved into an endemic dwarfed form *B. (Eobison) degiulii* on the geographically isolated Italian Peninsula. The “advanced” cranial morphology of *B. (Eobison) degiulii* [4] in this case may represent specific (paedomorphic?) characteristics resulted from the dwarfing process. It is necessary to mention that *B. (Eobison) degiulii* is associated in the fauna from Pirro Nord with the diminished form of a primitive fallow deer similar to *Dama vallonnetensis*, but reduced in size [6].

B. menneri is a large boreal cursorial form, which dispersed in Central and Southeastern Europe by the end of Villafranchian, but failed to overcome the Alpine mountain belt and colonize southern regions of Europe and Transcaucasia. Possibly, the origin of *B. menneri* is related to *Bison (Eobison) palaeosinensis*. It seems that *Bison menneri* is a forerunner of larger and more robust, but still quite long limbed *Bison* from Middle Pleistocene of the Tiraspolian gravel (Croitor, work in progress). It is not clear if *B. (Eobison) tamanensis* and *B. menneri* coexisted in Tamanian faunas or not. One cannot exclude that those two species represent different stages of the local faunal evolution.

Apparently, one can recognize two Early Pleistocene archaic lineages of bison: the boreal lineage *B. (Eobison) palaeosinensis* – *B. menneri* – *Bison sp.* from the Tiraspolian gravel and the southern lineage *B. (Eobison) sivalensis* – *B. (Eobison) georgicus* – *B. (Eobison) tamanensis* – *B.*

(*Eobison*) *degiulii* that evolved in Southern Eurasia (Indian Subcontinent and Mediterranean Area). The evolutionary divergence between those two archaic lineages of bison was caused by geographic obstacle created by the Himalayan Mountain massive or, in a broader sense, by the Alpine-Himalayan mountain belt. This evolutionary divergence produced the giant cursorial form that inhabited boreal open landscapes (*B. menneri*) and the lineage of smaller southern forms, which, probably, maintained more primitive cranial characters, were adapted to mountain forested environments and comparatively mild climate. The southern lineage of *Eobison* was able to overcome mountain obstacles and colonize southern European peninsulas; however, it could not overcome the climate barrier and disperse into the boreal latitudes of Eurasia. The “advanced” cranial characteristics of the endemic Italian diminished form *B. (Eobison) degiulii* may have a nature close to the insular “paedomorphic” process or represent a phenomenon of evolutionary parallelism.

Acknowledgements. I am thankful to Danilo Torre, George D. Koufos, and Lorenzo Rook who supported my fellowship projects and made possible the study of bison remains stored in the paleontological collections of the Universities of Florence and Thessaloniki. Special thanks to Vera Baigusheva who helped me and organized for me the access to the paleontological collections of the Azov Museum. Many thanks to Dimitris S. Kostopoulos and Vadim Titov for their valuable help during my work with collections. The visiting fellowships were supported by the CNR/NATO Science Program (Italy) in 1999 and 2005, and The Ministry of Economy/NATO Science Program (Greece) in 2001. The visit to the Azov Museum of Local Lore was supported by A.G. Side Fund Grant of the Linnaean Society of London (1999). I thank also Igor Nicoara and V. P. Pocatilov who provided access to the paleontological collection of the Moldavian Hydrogeological Expedition.

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**MATERIALELE CONFERINȚEI ȘTIINȚIFICE NAȚIONALE
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**Ediția a III-a,
consacrată aniversării a 80 ani de la nașterea
prof. univ., dr. hab. Alexandru LUNGU**

(06 - 08 octombrie 2016)

CHIȘINĂU, 2016