საქართველოს მეცნიერებათა ეროვნული აკადემიის მოამბე, ტ. 18, №3, 2024
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Palaeobiology

Genus *Prostrepsiceros* Major, 1891 (Bovidae) from the Udabno and Eldari Sites (Late Miocene, South Caucasus)

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(Presented by Academy Member David Lordkipanidze)

In this paper, fossil remains of *Prostrepsiceros* from the Eldari and Udabno sites: *P. vallesiensis* (Eldari) and *P. rotundicornis* (Udabno) are described. This is the first report of the genus from the region. These occurrences add in the distribution pattern of these species in the Balkano-Afghan province. The presence of *P. vallesiensis* suggests a Vallesian (MN10) age for part of the Eldari outcrop and fauna, while *P. rotundicornis* points to a Turolian age (MN11? MN12?) for the Udabno fauna found in the upper part of the section. The extreme scarceness of spiral-horned antelopes in Udabno and Eldari faunas is most probably related to the remoteness of open habitats from the floodplain developed along the regressing paleo-Kura Bay, where the Udabno and Eldari sites are located. © *2024 Bull. Georg. Natl. Acad. Sci.*

Prostrepsiceros, Udabno, Eldari, Late Miocene

Late Miocene sediments along the paleo-Kura Bay of the Eastern Paratethys Sea in the South Caucasus contain the earliest terrestrial fossil record from the Middle Kura Basin (MKB) [1]. Udabno (Georgia) and Eldari (Azerbaijan) are among the oldest sites in the MKB, where diverse vertebrate faunas have been discovered, including remains of the *dryopithecine Udabnopithecus garedziensis* Burchak-Abramovich and Gabashvili, 1945. Udabno and Eldari are large and complex sites with thick fossil-bearing sedimentary deposits. These fossiliferous layers were largely formed during the Khersonian stage (ca. 9.7-7.65 Ma, [2]) of the Eastern Paratethys. Their deposition is diachronous since it tracks sea retreat eastwards comprising sediments deposited mainly during regression and terrestrial phases of the Khersonian stage. As a result of sea regression, the terrestrial setting appears earlier in the west (Udabno) than in the east (Eldari). At the Udabno site, land emerged sometime at the end of the Bessarabian stage [1] (Bessarabian precedes Khersonian stage and is dated between ca. 11.8-9.6 Ma; [3]), while in Eldari land emerged during the Khersonian regression. At the Udabno site, fossils are found in the Eldari Formation (a continental particolored lithostratigraphic unit), and from the

Shiraki Formation (a huge succession of clay and sandstone) overlaying the latter. In the eastwardly located Eldari site, fossils are found in the so-called "30m thick sandstones" (a marker horizon underlying the Eldari Formation in the eastern part of the Middle Kura Basin) and in the overlaying Eldari and Shiraki Formations. There are correlation issues and questions regarding the detailed chronological framework of the MKB deposits which are currently under study.

Materials and Methods

This study embraces fossil collections from the Eldari and Udabno fossil sites held at the Georgian National Museum, in Tbilisi. The remains of *P. vallesiensis*, discussed below, were collected from the Eldari site in 1985-86. They come from an unknown stratigraphic level; still, the fossilization pattern (whitish color) might indicate that they come from the Eldari Formation, rather than the "30m thick sandstones" where fossils are brownish. The discussed horncore of *P. rotundicornis* was found in 2019, in the upper part of the Udabno section of the Shiraki Formation (GPS coordinates: 41°27'2.40"N, 45°23'47.19"E).

Abbreviations: TDb: transverse diameter at the base of horncore; APDb: anteroposterior diameter at the base of horncore; MKB: Middle Kura Basin. GNM-Georgian National Museum. All measurements are in millimeters.

Systematic Paleontology

Family BOVIDAE Gray, 1821

Tribe Antilopini Gray, 1821

Genus *Prostrepsiceros* Major, 1891

Type species *Prostrepsiceros houtumschindleri* (Rodler & Weithofer, 1890).

***Prostrepsiceros vallesiensis* Bouvrain, 1982**

(Fig. 1 – Ba-d, C)

Site: Eldari, Azerbaijan, South Caucasus.

Material: right horncore – GNM1 31-2013/75a (363-22); frontal fragment with left horncore base – GNM1 31-2013/75b (363-23). These specimens belong to the same individual.

Description. The right horncore appears to belong to a small-sized bovid, about the size of a gazelle. It shows a loose heteronymous torsion, mediolateral compression (GNM1 31-2013/75a – DAPb:28.4 mm, DTb:20.6 mm; GNM1 31-2013/75b – DAPb:27.3 mm, DTb:19.8 mm). The anteromedial keel is weak but noticeable without associating furrow and there are traces of a posterolateral keel. GNM1 31-2013/75a has a flat medial surface. The horncores are inserted above the orbit on short pedicles, gently curved backward and somewhat outwards. The demarcation of the horncore base is placed higher anteriorly than posteriorly, and is clearly visible laterally and posteriorly, while on the medial and anterolateral sides the relief is low. The long axis of the horncore base makes ca. 45° angle to the sagittal plane (possible to estimate on the GNM1 31-2013/75b specimen). Postcornual fossa is well marked, pear-shaped. Fronto-parietal suture passes just behind the horncores, supraorbital foramens are not preserved. Neither frontals, pedicles, or horncores are pneumatised.

Comparison. Medio-laterally compressed, heteronymously torsioned horncores make the Eldari antelope similar to forms included in the subgenus *P. (Prostrepsiceros)* Bouvrain, 1982. Two species in particular, *P. vallesiensis* and *P. vinayaki,* have comparable size to Eldari form, yet, morphologically Eldari specimens fit best *P. vallesiensis*.

Details of horncore characters are rather variable in *P. vallesiensis* [4-6]. Variability concerns expression of keels – combinations of blunt to sharp postero-lateral and anteromedial keels; degree of horncore compression – more compressed in females, torsion-females having looser torsion than males [4]; development of postcornual fossa from nearly absent to shallow. The following characters seem to be more stable: small supraorbital foramen not sunken into a pit (not preserved on Eldari material); the oblique position of the long axis of the horncore base to the sagittal suture (conforms with Eldari); the absence of furrow

along the anteromedial keel (conforms with Eldari). The above-listed character states differ between *P. vallesiensis* and *P. vinayaki*, a similar size antelope, with a spectacular biogeographic distribution known from Palaearctic, Oriental, and Afrotropical realms [7]. *P. vinayaki* in contrast to *P. vallesiensis* has relatively large supraorbital foramina in round to pear-shaped pits, a more perpendicularly placed horncore long axis to the sagittal plane (does not conform with Eldari), and a furrow along the medial keel (not present in Eldari). Considering this evidence the Eldari antelope can be attributed to *P. vallesiensis*. Morphologically cross section from the Eldari site (GNM1 31-2013/75a) is closest to the Middle Sinap (MN9) horncore from the loc. 91.92 455 (fig. 15.12, *Prostrepsiceros* sp. [5], accepted as *P. vallesiensis* by Kostopoulos [4]).

Prostrepsiceros rotundicornis (Weithofer 1888)
(Fig. 1 – Aa-d)
Site: Udabno-Lavra, Georgia, South Caucasus.
Material: left horncore fragment – GNM1 32-2013/1500.

Description. The horncore belongs to a medium-sized antelope, larger than the previously described *P. vallesiensis*. It has a heteronymous torsion and is inserted above the orbit. In profile, the horncore is somewhat curved backward; divergence would not have been strong. The pedicle is extremely short; a large supraorbital foramen opens in a deep supra-orbital pit rather close to the horncore base (this area is damaged and the shape of the pit cannot be estimated). The distance between the supraorbital foramen and horncore base is 14 mm. Postcornual fossa is like a shallow depression. The cross-section at the base is a rostro-caudally weakly compressed ellipse (DTb:34.3 mm, DAPb:28.6 mm), with almost flat posteromedial surface. The horncore surface is ornamented by shallow thin grooves, more pronounced and regular on the lateral and posterior sides. A blunt keel starts postero-laterally above the postcornual fossa; upwards it is associated by a shallow furrow medially. On the lateral side, there are well-marked notches along the horncore base. There are no traces of frontal or horncore pneumatization.

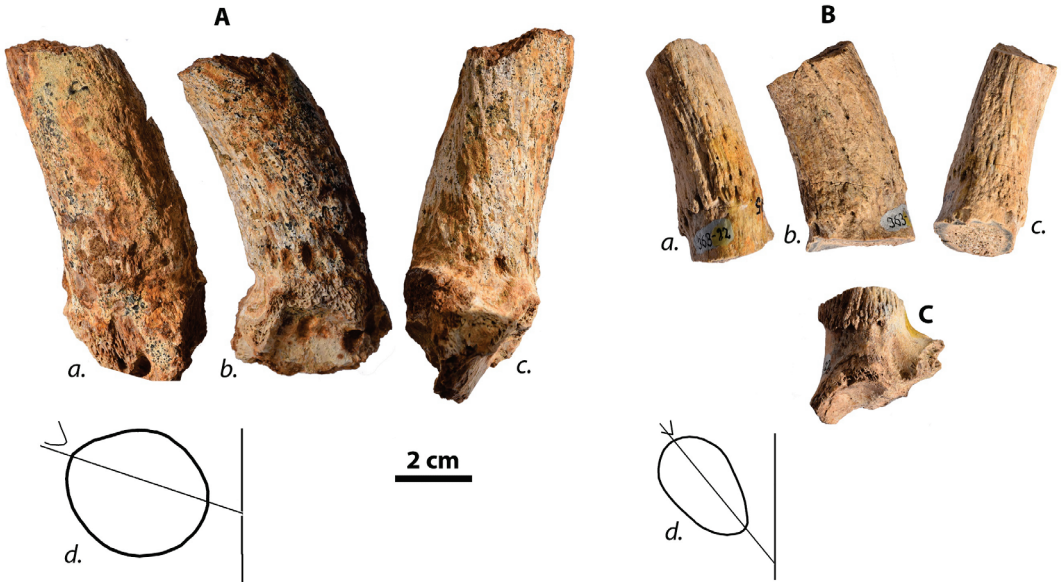

Figure. A – *Prostrepsiceros rotundicornis* horn core GNM1 32-2013/1500 from Udabno: a. anterior view, b. lateral view, c. posterior view, d. cross section at the base; B – *Prostrepsiceros vallesiensis* horn core GNM1 31-2013/75a from Eldari: a. anterior view, b. lateral view, c. posterior view, d. cross section at the base. C – *Prostrepsiceros vallesiensis* frontal fragment with horn core base GNM1 31-2013/75b from Eldari, posterior view.

Comparison. Rostro-caudally compressed, heteronymously twisted horncore makes the Udabno antelope similar to forms included in the subgenus *P. (Helicotragus)* Bouvrain, 1982. *P. axiosi*, and *P. zitteli* are readily excluded from comparison due to the absence of a sharp anterior keel. The remaining *P. fraasi* and *P. rotundicornis*, antelopes with weekly expressed keels differ from each other by horncore insertion and degree of divergence (uprightly vs. obliquely, strongly divergent from the base vs. slightly divergent in *P. fraasi* and *P. rotundicornis*, respectively), not reliably observable on the Udabno specimen, although they seem to be more like *P. rotundicornis*; by size *P. fraasi* appears larger than *P. rutundicornis*; the Udabno horncore is metrically comparable to the latter species. The absence of posterior keel in *P. fraasi* vs. the presence of a weak to strong posterior keel descending above the postcornual fossa in *P. routundicornis* conforms with the Udabno fossil. Sometimes the posterior keel is associated with a furrow apically in *P. rotundicornis*, as in Udabno. Other cranial characteristics of *P. rotundicornis* such as: shallow postcornual fossa and large supraorbital pits in deep depressions also affiliate the Udabno horncore to *P. rotundicornis*. An anterior keel – not observable on the studied horncore fragment from Udabno, cannot be used as a reliable character since it is rather variable in *P. rotundicornis*: if it is present, it is always very weak, the descending point of this keel varies from posteromedial (e.g. in Chomateri, [8]) to anteromedial. As a result, attribution of the Udabno horncore to a *P. rotundicornis* seems the most plausible.

Discussion and Conclusion

Various Late Miocene bovids exhibit twisted and spiraled horncores, especially among *Caprinae* and *Antilopinae*, commonly known as spiral-horned antelopes. They are important elements of the Balkano-Afghan province and beyond, first appearing in the early Vallesian (MN9) and becomeing especially diverse and abundant during Turolian faunas (MN11 MN12) [8]. Considering the time frame (MN10-MN11) of the earliest terrestrial faunas in MKB, their presence was highly expected; yet, they remained unknown. The recent revision of historical collection and newly collected fossils confirmed this expectation.

The genus *Prostrepsiceros* to which Eldari and Udabno fossils are ascribed, is among the earliest Antilopini with an heteronymous torsion. The earliest evidence of the genus comes from the early Vallesian (MN9) of Turkey (Middle Sinap, [5]) and the last occurrences not exceeding the Mio-Pliocene boundary [9]. *Prostrepsiceros* has a remarkably wide paleobiogeographic distribution, embracing the Greco-Irano-Afghan biogeographic province of the Palaearctic, as well as the Oriental (Pakistan) and Ethiopian realms (Arabia) [4,5,7].

Two groups are distinguished within the genus by Bouvrain [6]: (1) with mediolaterally compressed horncores (subgenus *P. (Prostrepsiceros)* Bouvrain 1982) comprising *P. houtumschindleri* Rodler et Weithofer, 1890, *P. syridisi* Kostopoulos and Koufos, 1996, *P. vinayaki* (Pilgrim, 1939), and *P. vallesiensis* Bouvrain, 1982, and (2) with rostro-caudally compressed horncores (subgenus *P. (Helicotragus)* Bouvrain, 1982) comprising *P. rotundicornis* (Weithofer 1888), *P. zitteli* (Schlosser 1904), *P. fraasi* (Andrée 1926), and *P. axiosi* Kostopoulos 2004. Representatives of both groups are identified in the earliest fossil assemblage from the MKB. *Prostrepsiceros*, as currently understood, is polyphyletic [4], especially as regards the second group – *P. (Helicotragus)* and the division of *Prostrepsiceros* into the mentioned subgenera suggested originally by Bouvrain [6] is largely abandoned by later authors.

P. vallesiensis is a quite rare, strictly Vallesian species, known from MN9-MN10 of Turkey (Sinap) [5] and Greece (Ravin de la Pluie, MN10) [4]. Reasonably, the presence of *P. vallesiensis* points to a Vallesian Land Mammal Age (MN10, ca. 9.7-8.7Ma) for that part of the Eldari section. The general geological setting does not contradict this idea.

The second species, *P. rotundicornis* found in Udabno, comes from the Shiraki Formation. *P. rotundicornis* is one of the most widely distributed and common *Prostrepsiceros* species in the middle Turolian (MN12) faunas of the Balkano-Afghan province [9]. The earliest representatives are known from the earliest Turolian (Ravin des Zouaves 5, [6]). The presence of this species points to a Turolian age (MN11?, MN12?) for the upper part of the Udabno outcrops.

The extreme scarcity of spiral-horned antelopes is a striking feature of Udabno and Eldari faunas. A plausible explanation can be the remoteness of the spiral-horned antelope habitats (more open, seasonal landscapes) from the floodplain developed along the regressing Kura paleo bay covered with mosaic of isolated and semi-isolated basins, i.e., lakes, lagoons, and river networks.

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პალეობიოლოგია

გვარი *Prostrepsiceros* Major, 1891 (Bovidae) უდაბნოსა და ელდარის ადგილსაპოვებლებიდან (ზედა მიოცენი, სამხრეთ კავკასია)

მ. ბუხსიანიძე

საქართველოს ეროვნული მუზეუმი, თბილისი, საქართველო

(წარმოდგენილია აკადემიის წევრის დ. ლორთქიფანიძის მიერ)

ნაშრომში აღწერილია გვარი *Prostrepsiceors*-ის ნამარხი ნაშთები ელდარისა და უდაბნოს ადგილსაპოვებლებიდან: *P. vallesiensis* (ელდარი) და *P. rotundicornis* (უდაბნო). ხვეულრქიანი ანტილოპების აღნიშნული გვარი აქამდე ცნობილი არ იყო სამხრეთ კავკასიის ნამარხ ხერხემლიანთა ფაუნებიდან, თუმცა მისი არსებობა სრულებით მოსალოდნელი იყო, რადგანაც *Prostrepsiceors*-ი ფართოდ გავრცელებული და დივერსიფიცირებული გვარია მთელს ბალკანეთ-ავღანეთის რეგიონში. *P. vallesiensis* და *P. rotundicornis*-ის დადგენა ელდარისა და უდაბნოს ფაუნებში ავსებს აღნიშნული სახეობების გეოგრაფიული გავრცელების სურათს. ბიოსტრატიგრაფიული თვალსაზრისით *P. vallesiensis* არსებობა ელდარში ვალეზიურ (MN10)

ასაკზე მეტყველებს, ხოლო უდაბნოში *P. rotundicornis* მიუთითებს უდაბნოს ადგილსაპოვებლის ზედა შრეების ფაუნის შედარებით გვიანდელ, თუროლიურ (MN11?, MN12?) ასაკზე. ხვეულრქიანი ანტილოპების ნამარხი ნაშთები ძალზე იშვიათია უდაბნოსა და ელდარის ნამარხ ფაუნებში. ეს დაკავშირებული უნდა იყოს იმასთან, რომ შედარებით ღია ლანდშაფტი, რომლის ბინადრებიც იყვნენ გვიანმიოცენური ხვეულრქიანი ანტილოპები, შედარებით შორს უნდა ყოფილიყო მტკვრის პალეოუბის ნაპირას არსებულ მდინარეებით დაქსელილ დაბლობისაგან, რომლის ამგებ დანალექ ქანებში გვხვდება უდაბნოსა და ელდარის ნამარხი ფაუნის ნაშთები.

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