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LARGE-SIZED DEER FROM THE EARLY PLEISTOCENE OF SOUTH-EAST EUROPE

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Abstract. The present paper brings summarized data on early Pleistocene large-sized deer from Balkan and Black Sea Areas of Europe. Several stocks of giant deer occur in Europe along the gradual climate aridization: a poorly known yet lineage of *Arvernoceros* that is characterized by a significant size variation, and two sister lineages of the genus *Praemegaceros* presented by species *P. obscurus* and *P. pliotarandoides*. Taxonomical problems, synonymy, morphology and distribution of the early Pleistocene large-sized deer are discussed in the article.

Keywords: Early Pleistocene, Europe, Cervidae, Morphology, distribution.

INTRODUCTION

The early Pleistocene climate shifts in Europe brought a variety of large-sized ruminant forms. The large body size in ruminants must be regarded here as a general evolutionary trend correlated to biological advantages in open landscapes that progressively became predominating in Europe during early Pleistocene. The systematical variety and numerous phylogenetic lineages of early Pleistocene large-sized deer suggest that this faunal group finely mirrored the environmental changes in Europe. However, the knowledge on morphology, systematics and distribution of early Pleistocene large-sized deer is still incomplete and confused for the present moment. Many finds of fossil deer from North Caucasus, Black Sea Area and Balkan Area, mostly fragmented, are still poorly determined and understood. The interest of fossil deer identification from the mentioned region is particular, as we are dealing in this case with records of early expansion of cervids from Asia to Europe. The present work is an attempt to clarify the systematics and distribution of large-sized deer in South-East Europe, as well as the revision of some cervid finds with unclear systematical determination.

SYSTEMATICAL DESCRIPTION

Genus *Arvernoceros* Heinz 1970

Numerous mostly fragmented remains of a very particular large-sized deer are reported from early Pleistocene deposits (Khaprovian, Psecupsan and, apparently, Tamanian faunal units) of South-East Europe. The remains of this form (or forms) of deer occurs in the geological time span 1 Ma - 2 Ma approximately and are characterised by size variation from rather small to large (Croitor & Kostopoulos, in press). The remains of those cervid forms are characterised by rather primitive morphology of dentition, with simple P_4, relatively short lower premolar series. The antlers are particular in their morphology and rather simple, with palmed first tine inserted at a long distance from the burr and a small terminal palmation. This type of antler morphology is found in *Arvernoceros ardei* from middle Villafranchian of France, a fact that gives reasons to refer the antlers and the specimens that may be associated with them to the genus *Arvernoceros*. The fossils ascribed to late Villafranchian *Arvernoceros* are not completely understood yet because of their fragmentary character and unclear geological context so it is preferably to discuss separately the finds from each locality.

Arvernoceros verestchagini David 1992

The description of this species was based on a very large complete antler from Salcia quarry, Moldova (David, 1992). The stratigraphical context of the Salcia site is still not clear enough, so we can just assume that the geological age of this specimen may correspond to the early stage of Psecupsan (=Odessan) faunal assemblage, although the mixed character of the fauna from Salcia quarry is very probable (Abbazzi et al., 1999). Besides the extremely large size, the species is characterised by a cylindrical shape of antler beam, a very high inserted first tine, which is extended into a small palmation terminated by three prongs. The antler beam turns backward in the area of first ramification. Its distal third is gently curved toward the anterior and some-what compressed latero-medially. The terminal part of antler is broadened into a small palmation with two prongs (Fig. 1). The holotype is only a specimen from Salcia ascribed to the species, so we are not able to make conclusion on morphological and size variation of this species. The above-mentioned problems make quite difficult the use of this species name for the fragmented fossil remains from other sites.

Flerow (1962) proposed the new genus and species name *Pseudalces mirandus* for a fragmented skull of a very large deer found in the Kosjakinskij quarry outcrops (South Russia) with mixed fauna of Villafranchian type. Besides the extremely large size, the fragmented skull is

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characterised by a long orbito-frontal part, reduced preorbital pits, comparatively large orbits (larger than those in *Megaloceros*) and a particular shape of frontal bones depressed before pedicles and convex between orbits (Flerow & Shevyreva, 1963). The similar particular shape of frontal bones is found in the antlered frontlet from Liventzovka ascribed by Bajgusheva (1992) to *Arvernoceros sp*. (see below). The specimen from Kosjakinsky quarry may belong to a giant cervid similar or even identical to *Arvernoceros* from Moldova. In this case, the species name *Arvernoceros verestchagini* David 1992 fall in the synonymy list of "*Pseudalces*" *mirandus* Flerow 1962. However, the insufficient data for comparison does not allow making a definite conclusion.

Arvernoceros cf. *verestchagini* DAVID 1992 from Greece

Synonymy:

1997 *Megaloceros sp*. (partim) – Kostopoulos: p. 846, fig. 1a, b, d, e, f.

The rather fragmented material of a giant *Arvernoceros* has been yielded by a early-Pleistocene site Apollonia, North Greece (Kostopoulos, 1997; Croitor & Kostopoulos, in press). The material consists on few fragments of antlers, post-cranial bones and series of upper and lower dentition, so the comparison with type specimen of *A. verestchagini* from Moldova is not possible. The left maxillary bone APL-274 with complete upper cheek tooth row (Fig. 2, A) is the best-preserved specimen that is not affected by heavy tooth wear, although the advanced stage of wearing could remove some morphological details. The lingual side of P^2 is split, so protocone and "hypocone" are clearly separated from each other. The enamel of interior side of the "hypocone" is folded, forming together with the metacone an enamel islet. The lingual slope of P^3 is grooved; however, the protocone and the "hypocone" are not separated here. The enamel of the interior side of the "hypocone" is folded. A small isolated enamel islet is present in the "hypocone". The lingual slope of P^4 has a shallow groove. The enamel of the interior side of the "hypocone" is folded as well. Upper molars are supplemented with an "entostyle" and a "hypoconal" spur. A small but clearly expressed cingulum is present in one M^3. The lingual slopes of all molars have some-what concave profile in the antero-posterior view, unlike that in *P. pliotarandoides* described below. The isolated upper right first molar APL-141 from Apollonia is smaller than the above described specimens and is affected by initial stage of wear. The enamel of this molar is characterized by presence of some additional folds. The posterior wing of its protocone is supplemented with a large additional enamel fold. The anterior and posterior wings have an additional enamel fold each as well. The entostyle is well developed.

The left ramus of lower mandible APL-384 belongs to a very large individual. The specimen does not display the mandibular pachyostosis. The symphisal part of mandible is situated below the level of grinding dental surface, unlike *Praemegaceros*, the symphisal part of which is placed above the grinding surface. P_3 is of simple morphology (Fig. 2, B) and its metaconid has a slightly broadened antero-posteriorly distal end. The parastilid and paraconid of P_3 are connected, closing a small enamel islet. P_4 is not molarized. The parastylid and paraconid of P_4 also close an enamel islet. The lingual part of the metaconid extends antero-posteriorly but it does not fuse with the paraconid or the entoconid, even in advanced stage of wear (APL-33). The entoconid is sloped backwards and get in touch with entostylid, without however to be fused together. An anterior fold is well developed in M_1 but it is quite weak in M_2. The "ectostylid" is well developed and high. It is laterally compressed in M_1 and column-like in M_2 and M_3. M_3 has only one ectostylid, positioned between "hypoconid" and protoconid. The lower tooth row length amounts to 188.0 mm; the premolar/molar ratio amounts to 63.0 %.

The late Villafranchian giant *Arvernoceros* from Moldova and Greece seems to be one of the largest fossil deer of Europe that exceeds the size of *Megaloceros giganteus*. The dentition of the Apollonian *Arvernoceros* maintains some particular characters that might suggest a more archaic morphology. Unlike *Praemegaceros pliotarandoides*, the upper dentition of *Arvernoceros* bears additional enamel folds in the interior sides of premolar "hypocone", as well as an "hypoconal" spur.

Arvernoceros giulii (Kahlke, 1997)

Synonymy:

1997 *Eucladoceros giulii* sp. nov. – Kahlke: p. 11, fig. 4-5.

The remains of a large-sized deer from Untermassfeld, Germany, described by Kahlke as a new species of the genus *Eucladoceros* should be mentioned here as well. There are no complete fully grown antlers reported for this species. The only known complete antler belongs to a young individual and may be interpreted as an early ontogenetical stage of *Arvernoceros* (Croitor & Kostopoulos, in press). The morphology of juvenile antler from Untermassfeld does not recall any ontogenetical stage of antler development of *Eucladoceros* with comb-like antlers figured by Bout & Azzaroli (1952). The hypothetical reconstruction of the fully-grown antler of *Eucladoceros giulii* (Kahlke, 1997: text-fig. 28) may be wrong as it is based on scant fossil fragments, which, most probably, belong to two different deer forms, *Arvernoceros* and *Praemegaceros*. Thus, the eucladocerine type of antler morphology in this

case is a matter of doubts. This deer is characterised by quite primitive dental morphology. One can assume that the large-sized deer from Untermassfeld should be ascribed to the genus *Arvernoceros* as well.

Arvernoceros sp. from Liventzovka, Azov Sea Area

Bajgusheva (1994) reported an antlered frontlet Nr. RGU-239Liv (stored in the Rostov State University) of a large deer from Khaprovian fauna of Liventzovka. The interfrontal suture before pedicles is very prominent; the frontal surface before pedicles is depressed. The pedicles are very long with round transversal cross-section. The antler beams are long, cylindrical, with only first tine preserved. The distal portion of antlers is broken off. The first tine is inserted high above the burr, not preserved, with compressed laterally base. Perhaps, with this frontlet may be associated very large lower mandibles from the same sample like, for instance, the specimen Nr. 836-1810/3. The length of lower dental series of this mandible amounts to 143.8 mm. The dentition is characterised by a comparatively short lower premolar series (the premolar-molar ratio amounts to 61.1%). The fourth lower premolar is simple. The symphisal part of mandible is situated below the level of grinding dental surface.

Arvernoceros sp. from Cişmichioi, Moldova

The lower mandible from the early Pleistocene of Cişmichioi, Moldova (CIS-19-188, *dx*, Institute of Zoology, Kishinau; Fig. 3) is quite similar to the specimens from Apollonia and Liventzovka in its morphology, and is very close to the specimen from Liventzovka it its size. The length of lower tooth row amounts to 149.7 mm. The symphisal part of mandible is situated below the level of grinding dental surface, the premolar/molar ratio amounts to 66.8%. The fourth lower molar is simple.

Arvernoceros sp. from Fântâna lui Mitinan, Romania

Prof. Radulesco kindly offered the cast of a left lower mandible ramus from Fântâna lui Mitilan. The geological age of this specimen is suggested as 1.6 Ma and is correlated to Odessan (= Psecupsan) mammal fauna from Eastern Europe (Radulesco & Samson, 1990). The mandible shape is similar to that of previous specimens, with low position of symphisal portion; however the size of specimen is rather small. The length of tooth row amounts to 136.5 mm. The premolar series is relatively short (premolar/molar ratio amounts to 54.7 %). Apparently, some other cervid remains from early Pleistocene of Romania (Slatina-2, Valea Grăunceanuiui) also may be ascribed to a deer of the genus *Arvernoceros*.

Genus *Praemegaceros* Portis 1920

Praemegaceros pliotarandoides (De Alessandri, 1903)

Synonymy:

1903 *Cervus pliotarandoides* sp. nov. – De Alessandri: p. 11, fig. 4-5.
1920 *Cervus* (*Praerangifer*) *pliotarandoides* (De Alessandri). – Portis: p. 137.
1948 *Cervus cf. pliotarandoides* (De Alessandri). – Gromov : p. 53.
1959 *Eucladoceros pliotarandoides* (De Alessandri). – Verestchagin: pp. 60-62, fig. 30.
1967 *Psekupsoceros orientalis* gen. nov. sp. nov. – Radulesco & Samson: p. 332, fig. 5.
1967 *Orthogonoceros verticornis* (Dawkins). – Melentis : p. 79, fig. 2 pl. 1-2.
1976 *Megaceros verticornis* (Dawkins). – Azzaroli : 485, pl. 1-2.
1979 *Megaceros* (*Megaceroides*) *verticornis dendrocerus* (Ambrosetti). – Azzaroli: p. 7.
1990 *Eucladoceros orientalis* (Radulesco & Samson). – Vislobokova : p. 158.
1993 *Megaceroides orientalis* (Radulesco & Samson). – Azzaroli & Mazza : p. 6, fig. 3.

This species appeared in Europe during the late early Pleistocene (Galerian) and is characterised by large heavy antlers with four dichotomously branched crown tines. The antler beam has a cylindrical cross-section; however it becomes compressed latero-medially in the region of posterior tine. The antler base and pedicle are oriented in the same direction. Further, the beam bends sideward and backward at the level of second tine. The distal portion of beam turns upward in the area of posterior tine, forming the characteristic right angle. The dichotomously branched crown tines are oriented more or less in a parasagittal plane. In many cases, the vestigial basal tine is presented above the burr on the anterior side of the antler base; however, it may be reduced as well. The second tine is inserted somewhat medially on the beam and bends outward. It is cylindrical and undulated. The transversal cross-section of pedicles is always rounded.

The upper dentitions of *P. pliotarandoides* from Psekups-Saratovskaya and from Apollonia display a set of advanced characters. The lingual wall of P^2 is not cleft, the interior wall of premolar “hypocone” is slightly folded, unlike those in *Eucladoceros* and *P. obscurus*. The upper molars have no protoconal fold which characterize *Eucladoceros* neither the spur of “hypocone” that may be found in both *Eucladoceros* and *P. obscurus*.

The lower mandible of *P. pliotarandoides* discovered in Apollonia (Greece) is characterized by typical for *Praemegaceros* elevated predental portion with symphisal portion situated above the grinding surface. The advanced stage of P_4 molarization in from also distinguishes this deer from *Eucladoceros* and *Arvernoceros*.

The type specimen of *P. pliotarandoides* was discovered in Galerian deposits of Italy. To this species were ascribed also all “*verticornis*”-like

remains recorded in the Galerian sites of Italy (= *Megaservices verticornis*: Azzaroli, 1976), early Pleistocene site Aliakmon (= *Orthogonoceros verticornis*: Melentis, 1967) from Greece, Psecupsian and Tamanian faunas of Ukraine (Mariupol) and South Russia (Psecups, Tamani) (= *Psecupsoceros orientalis*: Radulesco & Samson, 1967). Several more or less complete antlers of large deer from various early Pleistocene sites of Eastern Europe were reported by Alexeeva (1977) under the different names: *Eucladoceros sp*. (Psekups-Saratovskaya, South Russia; stored in the Paleontological Institute, Moscow), *E. cf. pliotarandoides* (Mariupol, Ukraine; the Regional Museum), and *E. cf. senezensis* (Khapry, South Russia; the Geological Institute, Moscow). All those specimens apparently belong to *P. pliotarandoides* (Fig. 4). Some fragmentary remains of antlers from Salcia (Moldova), such as the basal fragment of left antler inserted in pedicle and mentioned earlier as *P. verticornis* (Abbazzi et al., 1999), belong to *P. pliotarandoides* as well. This specimen is characterized by a circular cross-section of pedicle and a vestigial basal tine (Fig. 5).

P. verticornis, an advanced middle Pleistocene descent of *P. pliotarndoides*, shows a set of characters that allow distinguishing those two species. Unlike in *P. pliotarandoides*, its pedicles are strongly compressed in a dorso-ventral direction, the antlers are relatively larger, and the basal vestigial tine is always absent. Instead, an additional middle tine situated on the frontal side of beam between the second tine and the posterior tine is developed. The middle tine is always missing in *P. pliotarandoides*.

Praemegaceros obscurus (Azzaroli, 1953)

Synonymy:

1953 *Cervus obscurus* sp. nov. – Azzaroli, pp. 74-75, fig. 42-45.
1957 *Megaceros sp*. – Verestchagin, p. 54, fig. 19.
1967 *Allocaenelaphus arambourgi* sp. nov. – Radulesco & Samson, p. 324, fig. 1.
1977 *Eucladoceros cf. tetraceros* (Dawkins) – Aleksejeva, tab. 20.
1992 *Megaceroides boldrinii* sp. nov. – Azzaroli et Mazza, p. 29, fig. 4.
1995 *Megaceroides obscurus* (Azzaroli) – Abbazzi, p. 224.

Nomen oblitum:

1927 *Cervus megaceros mosbachensis* sp. nov. – Soergel, p. 375, tab. 17 fig. 1, 3, 4, tab. 18 fig 1, 3.

Unlike the previous two species, this deer is characterized by a very strong basal tine that springs off right above the burr (Fig. 6, 7). The antler beam is strongly sloped backward immediately from the burr. The transversal cross-section of the burr is irregular due to the well-expressed rib and the depression from the lateral side of the rib that extends from the basal tine to the second one. The second tine is also very large, even hypermorphous, always compressed dorso-ventrally, inserted on the medial side of beam, like in *P. pliotarandoides* and *P. verticornis*. The middle tine is present. The distal portion of antler turns upright in the area of posterior tine, like in the above-discussed two species. Several crown tines are inserted on the anterior side of the beam (Azzaroli & Mazza, 1993), thus, there is no dichotomous pattern of bifurcation found in *P. obscurus*. The transversal cross-section of pedicle is circular. The nasal bones do not reach behind the line connecting the anterior edges of orbits; the preorbital pits are deep and well developed. Upper molars always have a hypocone spoor. The hypocone enamel in premolars is not folded, however the lingual side of P^2 and P^3 are cleft (Croitor & Bonifay, 2001: p. 134, fig. 7). The shape of lower mandible is similar to *P. pliotarandoides*, with characteristic elevated predental portion, as it can be observed in the specimen Nr. 53-3 from Fârladeni, Moldova (Fig. 8). The lower fourth premolar is molarized.

The abundant remains of *P. obscurus* are recorded in the Forest Bed Formation, England (Azzaroli, 1953), the Early Pleistocene fauna of Brashov Depression, Romania (= *Allocaenelaphus arambourgi*: Radulesco & Samson, 1967) (Fig. 6), the faunas of Salcia (Abbazzi et al, 1999) and Fârladeni, Moldova (Fig. 7), the Late Villafranchian fauna of Pietrafitta (= *Megaceroides boldrinii*: Azzaroli & Mazza, 1993). Some of fragmentary remains of large-sized deer from Semibalki, South Russia may be also ascribed to this species (the unpublished material stored in the Azov Regional Museum), as well as the basal fragment of antler from Tzimbal (South Russia) reported as *Megaceros sp*. (Verestchagin, 1967: p. 55, fig. 19) and the basal fragment of an antler with strong basal tine from Ubeidiya, Israel, described by Guthrie (Gutrie, 198: p. 177, pl. III) as *P. verticornis*. The fragments of antlers from Cârnațeni, Moldova, ascribed by Aleksejeva (1977, tab. 20) to *Eucladoceros cf. tetraceros* (Geological Institute of Moscow, Nr. 734-1) and *Eucladoceros sp*. (Nr. 391-156, Nr. 391-29), apparently belong to *P. obscurus*. The cervid remains from Mosbach Sands, Germany, described by Soergel (1927) as *Cervus megaceros mosbachensis* are identical to the material referred here to *P. obscurus*, however, in order to avoid a taxonomical confusion, we suggest rejecting this species name as *nomen oblitum* because it was not in use more than 50 years.

CONCLUSIONS

The large-sized deer consist an important part of Early Pleistocene faunas of South-east Europe. The present stage of matter does not allow solving all taxonomical and systematical problems of this category of cervids, however, we can assume the presence of several different lineages of deer. The first one, *Arvernoceros*, is the most problematic one. It seems to be close to *A. ardei* from Middle

Villafranchian of France, however presented by different forms, which are quite variable in size at list. An extremely large form *A. verestchagini* David 1992 was found in Moldova and Greece. Perhaps, this form is close to *Pseudalces mirandus* Flerow 1962 from the North Caucasus Area. A small related form with extremely short premolars is recorded in Fântâna lui Mitinan, Romania. A large number of remains of a similar deer of intermediate size is discovered in various early Pleistocene sites of the Azov and Black Sea Area. Another similar form was reported from the Postvillafranchian site Untermassfeld, Germany, as a species *Arvernoceros giulii* (Kahlke, 1997). All those forms belong to a single phylogenetical stock and need a detailed study in future.

P. obscurus and *P. pliotarandoides* belong to two sister lineages that penetrated in Europe from Asian continent due to the gradual aridization of European climate during early Pleistocene. *P. obscurus* presents a more ancient and primitive stock that appeared in eastern Europe during the early stage of Psecupsian faunal development. This is a forest or woodland form that was replaced during the end Psecupsan and Tamanian age by the open and dry country adapted species *P. pliotarandoides*. *P. pliotarandoides* presents a more advanced and lineage of *Praemegaceros* and evolved into a successful middle-Pleistocene species *P. verticornis*.

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FIGURES

Fig. 1. *Arvernoceros verestchagini* David 1992: the shed antler from Salcia, Moldova; holotype (Institute of Zoology, Kishinau).

Fig. 2. *Arvernoceros* cf. *verestchagini* David 1992: A, the left maxillary bone APL-274 with complete upper cheek tooth row from Apollonia, Greece; B, the left tooth row P_3-M_3 of lower mandible APL-384 from Apollonia (Aristotle University of Thessaloniki), labial and occlusion views.

Fig. 3. *Arvernoceros sp*.: the right ramus of lower mandible CIS-19-188 from Cişmichioi, Moldova (Institute of Zoology, Kishinau) and the occlusion view of lower fourth molar P_4.

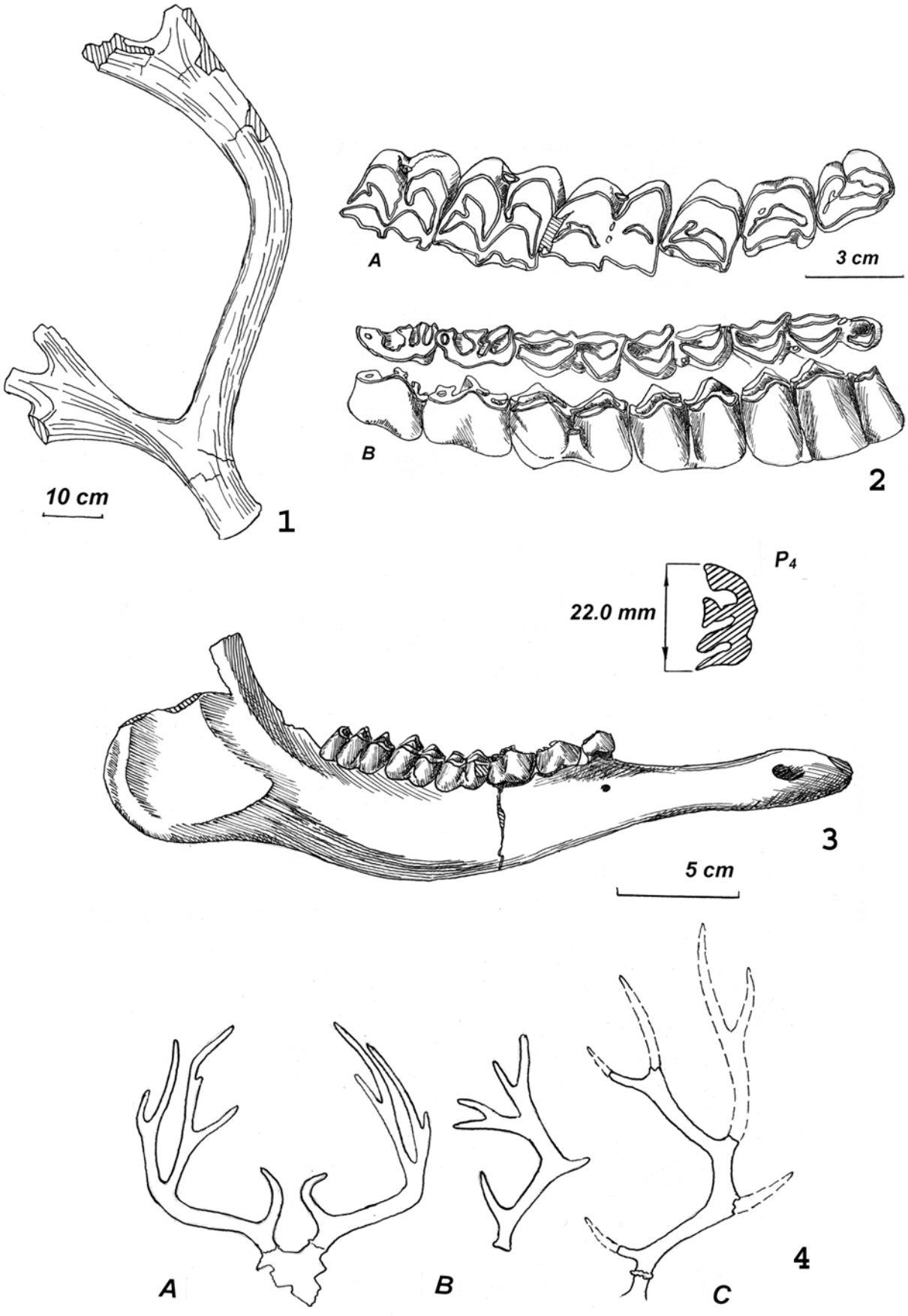
Fig. 4. *Praemegaceros pliotarandoides* (De Alessandri, 1903) from various sites (adapted and modified from Aleksejeva, 1977): A, an antlered frontlet from Psekups-Saratovskaya, South Russia; (Paleontological Institute, Moscow; = *Eucladoceros sp*.: Aleksejeva, 1977); B, a shed antler from South Ukraine (Regional Museum of Mariupol; = *E. cf. pliotarandoides*: Aleksejeva, 1977); C, an antler with fragment of frontal bone (Khapry, South Russia; Geological Institute, Moscow; = *E. cf. senezensis*: Aleksejeva, 1977); 1/10 of natural size.

Fig. 5. *Praemegaceros pliotarandoides* (De Alessandri, 1903): the basal fragment of left antler Nr. 52-431 with pedicle from Salcia, Moldova (Institute of Zoology, Kishinau).

Fig. 6. *Praemegaceros obscurus* (Azzaroli, 1953): A, the left antler with fragment of frontal bone from Forest Bed, England, the lectotype of *Cervus obscurus* Azzaroli 1953 (Natural History Museum of London); B, the right antler with fragment of frontal bone from Braşov Depression, Romania, the holotype of *Allocaenelaphus arambourgi* Radulesco & Samson 1967 (Institute of Speleology, Bucharest).

Fig. 7. *Praemegaceros obscurus* (Azzaroli, 1953): the basal fragment of antler Nr. 52-391 from Salcia, Moldova (Institute of Zoology, Kishinau).

Fig. 8. *Praemegaceros obscurus* (Azzaroli, 1953): the left ramus of lower mandible Nr. 53-3 from Fârladeni, Moldova (Institute of Zoology, Kishinau) and the occlusion view of lower fourth molar P_4.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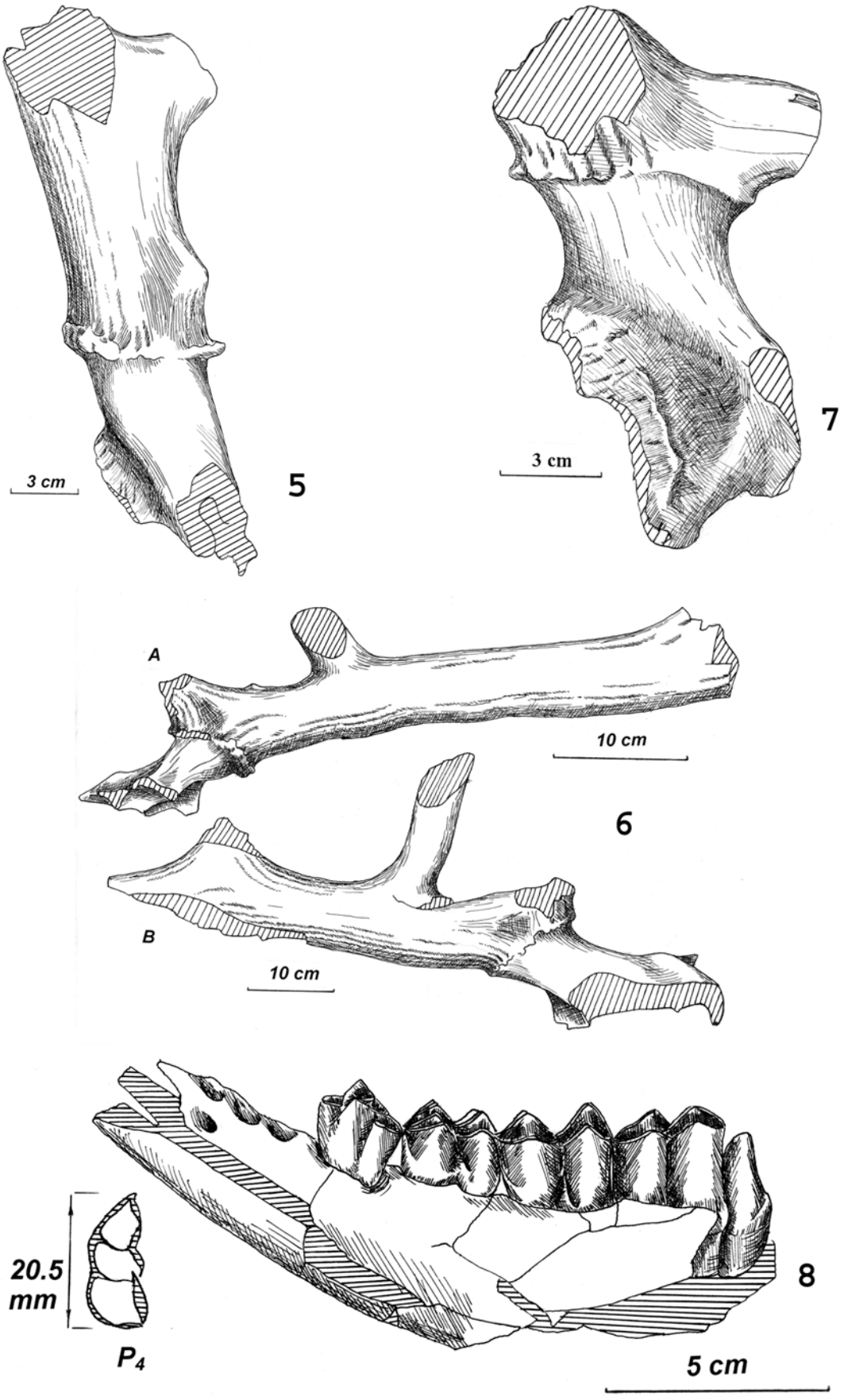
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