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A revision of “*Cervus*” *punjabiensis* Brown, 1926 (Cervidae, Mammalia) from the Upper Siwaliks of Chandigarh, India

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Abstract. This article proposes a revision of the best preserved fossil cervid recovered from the Upper Siwaliks, which, thus far, has been insufficiently described in the literature. The combination of antler and craniodental characters place the deer under study in the genus *Metacervocerus*, an extinct lineage with a vast Eurasian distribution and a sister phylogenetic relationship with the modern genus *Axis*. *Metacervocerus* is distinguished from *Axis* by its relatively longer upper premolar series and by the form of its second antler bifurcation which has a second tine that is inserted on the anterior side of the main beam. The new examination of the cranial and dental morphology of the specimen from the Siwaliks revealed peculiarities of its cranial and dental morphology that clearly distinguish *Metacervocerus punjabiensis* from *M. shansius* from the Late Tertiary of China. The article provides a taxonomic and evolutionary evaluation of craniodental characters of the type specimen of *M. punjabiensis*, and an analysis of the evolutionary significance of specific antler characteristics, as well as the phylogenetic relationships of the genus *Metacervocerus*.

Key words. Early Pleistocene, Eurasia, Cervidae, *Metacervocerus*, morphology, taxonomy.

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1. Introduction

Modern cervids from the Oriental Zoogeographic realm represent an important and diverse group (up to 20 species) of ruminants and play an important role in the modern ecosystems of the Indian Subcontinent (Bibi and Métais, 2016). The relatively late dispersal to and diversification of cervids in the Indian Subcontinent is an interesting and important paleobiogeographic event that changed the ecological character of the local herbivore paleoguild and provides a significant biostratigraphic marker in the Siwaliks paleontological record (Nanda, 2013). Despite the long history of research since the first description of cervid remains from the Siwaliks was published by Lydekker (1876), the paleontological history of cervids from Siwaliks is still insufficiently known and many species remain poorly defined. The Siwalik cervid species described by Lydekker (1876) were based on poorly preserved dental remains that resulted in confusion over multiple taxa in subsequent publications (Croitor, 2018). The poor preservation of Siwalik cervid type specimens did not allow researchers to associate well-preserved antlers discovered later with those dental and mandibular remains (Azzaroli, 1954).

Cervus punjabiensis Brown, 1926 from Chandigarh, Indian Siwaliks, is a lucky exception, since this species is based on an antlered skull with partially preserved upper cheek tooth rows. Brown (1926) provided a short species diagnosis, noting the high-crowned cheek teeth as a distinguishing morphological peculiarity of this cervid. The comparison of this dentition with those of Lydekker's (1876) cervid species from the Siwaliks confirmed the species status of the deer from Chandigarh (Brown, 1926). According to Brown (1926), *Cervus punjabiensis* is clearly closely related to modern *Axis axis* and *Rusa unicolor*, and shows a fairly close resemblance to *Cervus pardinensis* Croizet et Jobert, 1828 from the Pliocene of Perrier-Etouaires, Central French Massif. Teilhard de Chardin and Trassaert (1937) noticed an "impressive" similarity between *Axis shansius* from the Late Tertiary of China and *Cervus punjabiensis*. According to Azzaroli (1954), the available data are not sufficient to determine the phyletic position of the deer from Chandigarh. After the critical study published by Azzaroli (1954), *Cervus punjabiensis* attracted little attention and its systematic position was not subject to much discussion. Only recently did Croitor and Stefaniak (2009) briefly discuss the taxonomy of *C. punjabiensis*. Taking into account the suggestion by Brown (1926) of a resemblance between *C. punjabiensis* and *Cervus pardinensis*, they included both species in the genus *Metacervocerus* Dietrich, 1938.

However, the original description of *Cervus punjabiensis* does not provide a full record of its morphological features and includes only few measurements. Such a superficial description of the well-preserved specimen from Chandigarh does not permit an adequate comparison of the deer in question

with similar remains from the Siwaliks and other parts of the Eurasian continent, such as *Axis shansius* from the Late Tertiary of China and *Metacervocerus rhenanus* from the Early Pleistocene of Europe. The aim of this paper is to provide a detailed description of the type specimen of *Cervus punjabiensis* and to reveal its morphological affinities and possible phylogenetic relationships with modern and fossil deer.

2. Material and methods

This study involves the holotype of *Cervus punjabiensis* (AMNH19911) stored in the Paleontology collections at the American Museum of Natural History, New York, as well as the following samples of Pliocene and Early Pleistocene *Axis*-like cervids from Europe:

- *Metacervocerus rhenanus* from the Early Pleistocene of Ceysaguet, France (collection numbers with CEY) stored in the National Museum of Prehistory, Les Eyzies-de-Tayac, France.
- The damaged skull IGF-1408 of *Metacervocerus sp.* from the Early Villafranchian of Montopoli, Lower Valdarno (Italy) stored in the Geological and Paleontological Museum of the University of Florence.
- The braincase MCV-161 of *Metacervocerus sp.* from the Early Pleistocene of Milcovu din Vale (Olt River Valley near Slatina, Romania) stored in the Laboratory of Paleontology of the University of Bucharest.

Tooth series lengths are measured at the dental crowns as a maximum value; tooth crown length is measured as a maximum value at the grinding surface; tooth crown breadth is measured at the crown base. The cranial measurements of modern and fossil deer involved in the comparative analysis are from Vislobokova (1990) and Croitor et al. (2018). The anatomical point that Vislobokova (1990) and Croitor et al. (2018) term “opisthocranium” is more appropriately called “inion”, which is the point at which the left and right parts of the nuchal crest meet.

We followed the morphological criteria for identifying a genus in cervid systematics described in Vislobokova (1990) and Croitor (2006). Those criteria generally correspond to diagnostic characteristics that are applied in paleontological studies (Vislobokova, 1990 and references therein), but may be considered to be a “splitting” approach in neontology.

We ran a multivariate cluster analysis of the diagnostic cranial, dental, and antler characters in order to estimate the taxonomic value of the selected characters and to find support for the systematic position of the Plio-Pleistocene *Axis*-like deer of Eurasia included in the present study. The hierarchical clustering paired group algorithm UPGMA was computed using the Jaccard Similarity Index for presence-absence data (PAST-3 application: Hammer et al., 2001). The cophenetic correlation coefficient is computed in

order to estimate how faithfully a dendrogram preserves the pairwise distances among the original, unmodeled data points (Farris, 1969). Since the available data on cranial morphology are incomplete, we included some assumptions in our dataset, such as missing upper canines in *Metacervocerus pardinensis*, *M. shansius*, and *M. punjabiensis*, and short nasal bones in *M. pardinensis* and *M. punjabiensis*.

We follow Vislobokova (1990) in the classification of advanced and primitive conditions for the characters used in the cluster analysis:

- 1) Shape of basioccipital: 0, wedge-shaped; 1, bell-shaped (broadened at the pharyngeal tuberosities);
- 2) Upper canines: 0, absent (advanced condition); 1, present (primitive condition);
- 3) Pedicles: 0, long (pedicle height exceeds the pedicle diameter; primitive condition); 1, short (pedicle height is smaller than, or equal to, the pedicle diameter; advanced condition);
- 4) Pedicles: 0, sloped backwards (primitive condition); 1, set vertically (advanced condition);
- 5) Terminal crown type: 0, absent, 1, present; this crown type is characteristic of modern red deer (*Cervus elaphus*) that in its simplest variant represents a simple fork composed of two equally-sized crown tines oriented towards the rostral end of the cranium, perpendicular to the axis body;
- 6) Posterior crown type: 0, absent, 1, present; this crown type is characteristic of modern fallow deer (*Dama dama*) that in its simplest variant represents several tines inserted on the posterior side of the beam;
- 7) Length of nasal bones: 0, short (the posterior edge of nasals does not reach the level of the anterior edges of the orbits; primitive condition); 1, long (the nasal bones extend behind the level of the anterior edges of the orbits; advanced condition);
- 8) Cingulum on upper molars: 0, absent; 1, present (specialized dental morphology);
- 9) Protoconal fold on upper molars: 0, absent; 1, present (specialized dental morphology);
- 10) Position of the first antler ramification: 0, low (more or less equal to the antler base diameter); 1, high (significantly exceeds the antler base diameter);
- 11) Height of the cheek teeth crowns: 0, brachydonty (primitive condition); 1, mesodonty (advanced condition);

12) Length of the orbitofrontal part of the skull: 0, short (the anterior edge of the orbit is situated above M^3 or M^2 ; primitive condition); 1, long (the anterior edge of the orbit is situated behind M^3 ; the advanced condition in the *Cervus* lineage);

13) Braincase shape: 0, unflexed (primitive condition); 1, flexed (advanced condition).

14) Antler bauplan type: 0, "inadaptative" (the anterior tine of the second bifurcation is longer than the posterior tine); 1, "adaptative" (the anterior tine of the second bifurcation is shorter than the posterior tine).

3. Systematic description

3.1. Taxonomy

Family Cervidae Goldfuss 1820

Subfamily Cervinae Goldfuss, 1820

Genus *Metacervocerus* Dietrich 1938

Type species: *Cervus pardinensis* Croizet et Jobert, 1828

Updated diagnosis from Croitor (2006): The braincase is long and little flexed. The pedicles are rather long (the pedicle length is not shorter than pedicle diameter) and sloped backward. The orbitofrontal region is short; the anterior edge of eye sockets reaches the level of M^2 . The size of orbits is normal. The bulla tympani are large and rounded. The basioccipital bone is broadened at its pharyngeal tuberosities. The upper molars have a well-developed or rudimentary cingulum. The lingual wall of upper molars is strongly oblique. The angle between the lingual and labial walls of the upper molars is wider than 40° . The upper premolar series is relatively long: the premolar/molar series ratio is higher than 70%. The upper canines are missing. The morphology of P_4 is primitive and not molarized. The antlers are three-pointed, with a basal tine situated distantly from the burr (the distance being not less than the antler beam diameter). The distal bifurcation is oriented in the parasagittal plane. The posterior tine of the distal bifurcation of the antlers is longer and stronger than the anterior one. The antler surface is not pearled.

Composition: *M. pardinensis* (Croizet and Jobert, 1828), Pliocene, Europe; *M. rhenanus* (Dubois, 1904), Early Pleistocene, Europe; *M. shansius* (Teilhard de Chardin and Trassaert, 1937), Pliocene-Early Pleistocene, China; *M. punjabiensis* (Brown, 1926), Early Pleistocene of Siwaliks, Indian Subcontinent.

Metacervocerus punjabiensis (Brown, 1926)

Synonymy:

1926 *Cervus punjabiensis* sp. nov.: Brown, p. 1, figs. 1-4.

1935 *Cervus punjabiensis* Brown, 1926: Colbert, p. 320, figs. 149-152.

1937 *Cervus (Axis) punjabiensis* Brown, 1926: Teilhard de Chardin and Trassaert, p. 48.

1954 '*Cervus*' *punjabiensis* Brown, 1926: Azzaroli, p. 82.

2002 *Axis punjabiensis* (Brown, 1926): Di Stefano and Petronio, p. 321, fig. 11.

2009 *Metacervocerus punjabiensis* (Brown, 1926): Croitor and Stefaniak, p. 34.

Type locality: two miles west of Chandigarh, India.

Type horizon: Upper Siwaliks, Pinjor Formation.

Holotype: the antlered braincase and partially preserved upper tooth rows (right P²-M¹, left M³) and parts of splanchnocranium (nasal bones, fragment of orbital rim) of a young adult male (AMNH19911).

Amended diagnosis: Body size is slightly smaller than that of the European red deer. Antlers with a relatively low insertion of the first (basal) tine (the first ramification height does not exceed the two-fold antler base diameter value); braincase is relatively narrow and long (the braincase breadth behind the pedicles attains ca. 80% of the bregma-inion distance); occipital part of skull is relatively broad (almost twice as broad as the braincase width); bullae tympani are oval-shaped and smooth; pedicles are long (pedicle length exceeds the pedicle diameter) and moderately divergent (angle of divergence is about 67°). Upper molars are devoid of cingulum (only a moderately developed entostyle is present) and supplemented with an additional fold of protocone and the "hypoconal spur" (= the additional enamel fold of the metaconule). On P² and P³ the protocone and metaconule are separated by an isthmus. The metaconule of the premolars is supplemented by an inner enamel fold.

3.2. Skull

The specimen from Chandigarh has a well-preserved braincase with pedicles and almost complete antlers (Figs. 1, 2, 3). The facial part of the skull is destroyed and only a few features (the middle portions of the nasal bones, part of left eye socket rim, the right maxillary bone with P²-M¹, and a small fragment of the left maxillary bone with M³) are preserved (Fig. 3 C). The basioccipital is broadened at its

pharyngeal tuberosities and therefore the overall contour of the bone is bell-shaped (Fig. 3 C). The bullae tympani are smooth and oval.

The braincase is relatively narrow and long compared to the cervids in the comparative sample, including *Metacervocerus rhenanus* and *M. shansius* (Tab. 1, Fig. 4). The ratio braincase breadth/bregma to inion length is 80.8% in the holotype of *M. punjabiensis*. The same ratio varies between 92.1 – 103.7% in *M. shansius* (n=4; according to measurements provided by Teilhard de Chardin and Trassaert, 1937), 102.7 – 110.8% in *M. rhenanus* (n=4), and 94.0-100.5% in *Axis axis* (n=4).

The pedicles are rather long and moderately divergent: the angle of pedicle divergence is ca. 67° (Fig. 1). The occipital part of skull is relatively broad, much broader than in European *Metacervocerus* (Table 1). The pedicles are sloped back from the face and lie in the plane of frontal bones. They are relatively long and apparently represent a feature correlated with a rather young individual (ca. 4 years of age according to Brown, 1926). Nonetheless, the relative length of pedicles in the deer from Chandigarh remains quite high when compared to the samples of *M. pardinensis* from Etouaires (from the Early Villafranchian of France) and *Metacervocerus rhenanus* from Tegelen (from the Late Villafranchian of the Netherlands). The pedicles of European *Metacervocerus* included in the present study are quite short compared to those of the deer from Chandigarh and *Metacervocerus shansius* from the Late Tertiary of China (Fig. 5). The relative length of the pedicles of the *Metacervocerus rhenanus* sample from the Early Pleistocene site of Tegelen is quite similar to that of the small sample of *Metacervocerus pardinensis* from the Early Pliocene of Etouaires and the slight difference may be caused by the small sample sizes and differences in the demographic compositions of the samples.

3.3. Teeth

It is difficult to estimate the relative size of the upper tooth row of the deer from Chandigarh because its braincase, the only available skeletal part for this comparison, is characterized by peculiar proportions (rather narrow braincase with broad occiput). Generally, the upper tooth row length is similar to the values for *M. shansius* and exceeds the length of the tooth row of *M. rhenanus* by ca. 15% (Tab. 1). *M. punjabiensis*, *M. shansius*, and *M. rhenanus* share characteristics such as a relatively long premolar series. This feature distinguishes the species of the genus *Metacervocerus* from modern fallow deer and axis deer (Fig. 6). The preserved teeth of *M. punjabiensis* generally are as large as those of *M. shansius* and show intermediate size between those of *M. rhenanus* and *Praeelaphus perrieri*, a rather advanced deer with four-pointed antlers from the Early Pliocene of France (Tab. 3, Figs. 7, 8). The scatter diagrams confirm that the upper cheek tooth row of *M. punjabiensis* is characterized by size and proportions very

similar to those of *M. shansius*. The relatively labiolingually broader cheek teeth of *M. punjabiensis* is the only difference that possibly may have a morphofunctional and evolutionary importance.

The protocone and metaconule (“hypocone” according to Heintz, 1970) of P² and P³ are separated by a thin isthmus and are supplemented with fine inner folding (Fig. 3 C). The large inner folds of all three upper premolars may be interpreted as accessory enamel folds of the metaconule. This pattern of upper premolar morphology is very close to that of *Metacervocerus rhenanus*.

M¹ is supplemented with a moderately developed entostyle, however, the continuous lingual cingulum as in *M. pardinensis* is not developed. The posterior wing of the protocone in M³ is supplemented with an additional large enamel fold as in *Metacervocerus pardinensis* (this enamel fold is not clearly visible on figure 4 from Brown, 1926). A similar enamel fold, but weaker, is also present on M¹. This additional protoconal fold is not maintained in the dentition of *M. rhenanus*. Teilhard and Trassaert (1937) do not mention this enamel fold in *M. shansius*, stating that the teeth of the Chinese form are “brachyodont, without any particular character”. The dental remains of *M. shansius* from Udunga described by Vislobokova et al. (1995) also are devoid of an additional protoconal fold.

3.4. Antlers

The antlers are three-pointed, with a smooth surface and a rather high insertion of the first ramification that exceeds the anteroposterior diameter of the antler base (Fig. 2). The angle of the first ramification is almost 90°. The antler beam is helicoidally shaped and bears a second bifurcation that roughly represents the upper third of the antler. The angle of the second ramification is ca. 35°. The posterior tine of the second ramification is much stronger and represents a continuation of the antler beam. The second ramification is oriented in the parasagittal plane. The transversal section of antler beam is circular or slightly ovoid.

The size of antlers of *M. punjabiensis* corresponds to the largest known antlers of *M. rhenanus*, but they are somewhat more robust (Fig. 9). The antlers of the type specimen of *M. punjabiensis* are still quite robust if compared to *M. shansius* and trophy antlers of modern *A. axis*, but are relatively shorter. Generally, the antler shape of *M. punjabiensis* is identical to that of *M. shansius* and *M. rhenanus*. The only distinguishing feature between *M. punjabiensis* and *M. shansius* is the much higher position of the first ramification in the latter species.

4. Discussion

4.1. Cranial characters

The deer from Chandigarh shares with *M. rhenanus*, *M. shansius*, and modern *Axis axis* the smooth rounded shape of the bullae tympani, the bell-shaped basioccipital, and a smooth antler surface. However, the shape and proportions of the braincase in *M. punjabiensis* are very peculiar and distinguish this deer from all cervid forms involved in the study, including *A. axis*, *R. unicolor*, *H. porcinus*, *D. dama*, and *M. rhenanus*. The braincase of *M. punjabiensis* is very narrow and elongated, while its occipital is remarkably broad. According to Vislobokova (1990), a relatively long braincase is a primitive feature in cervids. The particularly narrow and long braincase in *M. punjabiensis* could be a primitive morphological condition maintained by the Siwalik lineage after the split from the main radiation of the genus *Metacervoceros*. However, the relatively long braincase in *M. punjabiensis* could also be a specialization since this character is combined with a broad occipital that represents an advanced feature in cervids (Vislobokova, 1990). Interestingly enough, the only cervid form that shows a similar combination of a narrow and long braincase and a very broad occiput is the giant deer *Megaloceros giganteus*: the braincase breadth / bregma toinion length ratio in the Irish sample varies between 85.4% and 101.0% (M = 92.5%, n = 5, NHML).

The relatively long pedicles is another primitive feature maintained by *M. punjabiensis*. Despite the young adult age of the type specimen from Chandigarh, its pedicles are still relatively longer than any in the large samples of *M. rhenanus* and are closer in size to the small sample of *M. shansius* specimens. Therefore, one can draw the conclusion that *Metacervoceros* from the Pliocene and Early Pleistocene of Europe are distinguished by the advanced evolutionary specialization of comparatively shorter pedicles.

M. punjabiensis is also distinguished from *M. shansius* in exhibiting the advanced feature of a stronger divergence of the pedicles: Vislobokova et al. (1995) report a small angle of pedicle divergence (36-40°) in a skull fragment of *M. shansius* from the Pliocene of Udunga, Transbaikal Region of Russia. The antlered skulls of *M. shansius* figured by Teilhard de Chardin and Trassaert (1937: pl. VI) are characterized by a similar angle of pedicle divergence.

4.2. Dental characters

The high crowned cheek teeth of *M. punjabiensis* reported by Brown (1926) correspond to the observations of Lydekker (1876) of remarkably high-crowned cheek teeth in Siwalik deer. Such a peculiar increase in tooth crown height or/and relative enlargement of total tooth row length is actually recorded in some fossil cervids adapted to xeric Mediterranean environments, such as *Praemegaceros*

(*Nesoleipoceros*) *cazioti* from the Late Pleistocene of Sardinia and *Haploidoceros mediterraneus* from the Late Pleistocene of the Iberian Peninsula (Caloi and Palombo, 1995; Croitor et al., 2018). However, the absolute and relative length of the upper tooth row in *M. punjabiensis* is similar to that of *M. shansius* and generally is consistent with the relative lengths of the upper tooth rows in cervines of similar body sizes.

A detailed analysis of the dental measurements reveal some features that require discussion of their evolutionary importance (Figs. 7, 8). *M. punjabiensis* is distinguished from *M. shansius* by slightly labiolingually broader tooth crowns (with the exception of an unusually short P²), a feature that is correlated with a more primitive brachyodont morphological condition (Vislobokova, 1990). Therefore, the cheek teeth of *M. punjabiensis* seem to be more primitive than those of *M. shansius*, taking into consideration the relatively broad dental crowns and more complicated enamel folding. The statement regarding the peculiar grazing specializations of Siwalik cervids, apparently, is based on bovid remains misidentified as cervids (Croitor, 2018 a) and therefore should be reconsidered.

The relatively long premolar series in *M. punjabiensis*, (the premolar/molar series length ratio is 75.2%) *M. shansius* (78.4%, n=2), and *M. rhenanus* (72.2-85.7% in the sample from Ceyssaguet, n=6) should be regarded as a morphological feature characteristic of the genus. The relative length of upper premolars in modern *A. axis* is much shorter (65.3%, n=4, NHML) and apparently should be regarded as an advanced morphological condition. Therefore, the upper dentition of *M. punjabiensis* is generally characterized by primitive features such as a relatively long premolar series, labiolingually broad tooth crowns, and complicated enamel folding.

4.3. Antler morphology

The antlers of *M. punjabiensis* show a great similarity to antlers of *M. shansius*, *M. pardinensis* and *M. rhenanus* in the parasagittal orientation of the distal antler fork, the stronger posterior tine of the distal fork, and the smooth surface of the antler. The difference in the height of the first tine insertion between *M. punjabiensis* and *M. shansius* pointed out by Teilhard de Chardin and Trassaert (1937) may be of minor importance, however we prefer to maintain this morphological feature in the species diagnosis. The smooth antler surface in *M. punjabiensis* resembles the morphology of *Axis axis*, *M. pardinensis* and *M. rhenanus* from the Pliocene and Early Pleistocene of Europe, but distinguishes these taxa from *R. unicolor*, *R. timorensis*, and *H. porcinus*.

The strong posterior tine of the distal bifurcation that represents a continuation of the main beam in *M. punjabiensis* is the most remarkable morphological feature that distinguishes the Siwalik deer from modern *A. axis*. This difference was noticed by Teilhard de Chardin and Piveteau (1930) who termed the three-pointed antlers with a longer posterior tine of the distal fork as “*aristotelis* type”. Correspondingly, the three-pointed antlers with the longest anterior tine of the distal fork are classified as “*hippelaphus* type” (*ibidem*). Later, Teilhard de Chardin and Trassaert (1937) called the three-pointed antlers with a stronger posterior tine of the distal bifurcation an “adaptative” type that, according to the cited authors, represents a transitional evolutionary stage between three-pointed and more advanced antlers of the “*Pseudaxis-elaphus* type”, i.e. the advanced type of antlers with trez (middle) tines and distal crowns. Apparently, the “adaptative” (or “*aristotelis*”) type of antlers represent the development of a three-pointed evolutionary stage of antlers in the evolution of an additional tine on the anterior side of the main antler beam. Therefore, the anterior tine of the second bifurcation should be regarded as a homolog of the trez tine in modern red deer (*Cervus elaphus*) and fallow deer (*Dama dama*). The trez (or middle) tine appears in the evolution of the subfamily Cervinae quite early and coincides with an increase in body size (Geist, 1971). Apparently, the development of this tine in the early stages of cervid evolution increases the safety of combatting stags that attained a certain body mass threshold that increases the risk of lethal wounding (Croitor, 2020). The trez tine or its analogs (for instance, in *Praemegaceros*) normally are found in cervines from middle latitudes and they most probably represent an additional adaptation to increase the survivorship of rutting males, which are already exposed to the stressors of cold seasons and a seasonal drop in forage in temperate latitudes. Therefore, the antler bauplan in *M. punjabiensis* suggests that this is a cervid originating from middle latitudes. The “*aristotelis*” type of antlers apparently evolved independently in several lineages. At least, one can assume the independent development of this type of antler in the extinct genus *Metacervocerus* and in modern *Rusa timorensis*, which is phylogenetically related to *C. elaphus* (Pitra et al., 2004).

The “inadaptative” (fide Teilhard de Chardin and Trassaert, 1937), or “*hippelaphus* type” of antlers represent another direction of antler evolution: the three-pointed stage of antlers is achieved by the development of a third tine inserted on the posterior side of the antler beam. The early stage of this evolutionary direction is represented by *A. axis* and the advanced evolutionary stage can be illustrated by *Rucervus* that possesses a complicated distal crown composed of simple and bifurcated tines inserted on the posterior side of the main beam. Cervids of this type do not possess the middle or trez tine and all of them are large-sized inhabitants of tropical latitudes. As in the case of “adaptative” antlers, the “inadaptative” type evolved independently in several lineages and similarities can be attributed to

biogeographic rather than phylogenetic factors. Deer with “inadaptative” antlers may evolve analogs of the middle tine after the development of a distal crown. This is the case in *Praemegaceros obscurus* from the Early Pleistocene of Europe that evolved from a South Asian forerunner similar to modern *Panolia eldii* (Croitor, 2018 b).

4.4. Systematic position and phylogenetic relationships

Azzaroli (1954) noticed that the relatively high tooth crowns of *M. punjabiensis* rule out the possibility of a direct phylogenetic relationship between *M. punjabiensis* and modern *Rusa unicolor* and *Axis axis*. A close affinity of *M. punjabiensis* with *M. pardinensis* (Croizet and Jobert, 1928) from the Pliocene of Europe was suggested by Brown (1926) and Teilhard de Chardin and Trassaert (1937). According to the current study, none of the craniodental features strictly contradict the direct phylogenetic relationship between *M. punjabiensis* and *A. axis* since all morphological characters available for study show a more primitive condition in the Siwalik deer. The antler bauplan is the only characteristic that rules out the possibility of a direct phylogenetic relationship between *M. punjabiensis* and *A. axis*. The example of *Rusa unicolor* and *R. timorensis* suggests that both “*aristotelis*” and “*hippelaphus*” types of antler bauplans can evolve in the same genus, although *Rusa* in its traditional understanding seems to be a paraphyletic taxon (Pitra et al., 2004). The peculiar braincase shape of *M. punjabiensis* rather suggests that the Siwalik deer is more distantly related to European and Chinese *Metacervocerus* forms.

The systematic position and phylogenetic relationships of *M. pardinensis* have been the subject of discussion and contradictory opinions. This cervid has been related to modern *Rusa unicolor* (Pomel, 1853; Di Stefano and Petronio, 2002) and *Axis axis* (Dawkins, 1878). It has also been assigned to the genus *Cervus* (de Vos et al., 1995) and placed the arbitrary group *Cervus sensu lato*, stressing the uncertain generic attribution of this cervid form (Heintz, 1970).

Dietrich (1938) created the subgenus *Cervus (Metacervocerus)* with *Cervus pardinensis* Croizet and Jobert, 1928 as the type species. However, he included in the synonymy of *C. pardinensis* a long list of species that makes the genus definition quite confused: *Cervus etueriarum* Croizet and Jobert, 1928 (which is regarded now as a junior synonym of *Praeelaphus perrieri*: Heintz, 1970), *Cervus perrieri* Croizet and Jobert, 1928 (which is included now in the genus *Praeelaphus* Portis: Croitor, 2017), *Cervus issiodorensis* Croizet and Jobert, 1928 (which is regarded now as a junior synonym of *Praeelaphus perrieri*: Croitor, 2017), and *Cervus rhenanus* Dubois, 1904 (which is regarded now as a valid species and included in the genus *Metacervocerus*: Croitor, 2006). Radulesco and Kisgyörgy (1970) elevated *Metacervocerus* to genus level.

Azzaroli (1992) included all small-sized Plio-Pleistocene deer from Western Europe in the new genus *Pseudodama* with *Dama nestii nestii* Azzaroli, 1947 as a type species. According to Azzaroli (1992), '*Pseudodama*' *pardinensis* is the oldest species in the genus. However, Azzaroli (1992) admits that *Pseudodama* may belong together with *Dama* in the same stem group, but that the direct relationship between those two genera cannot be demonstrated. Most researchers regard *Pseudodama* as a polyphyletic taxonomic group (de Vos et al., 1995; Di Stefano and Petronio, 2002; Croitor, 2006), however, opinions on which taxa should be grouped in *Pseudodama* are divergent. According to one of the authors of the present study, the genus name *Pseudodama* should be restricted to the type cervid form *Dama nestii nestii* Azzaroli, 1947 and is a junior synonym of the genus *Cervus* Linnaeus (Croitor, 2006). *Dama nestii eurygonos* Azzaroli, 1947 actually belongs to the genus *Dama*, while the *Axis*-like small cervids with three-pointed antlers, *Cervus pardinensis* and *Cervus rhenanus*, should be included in the genus *Metacervocerus* (Croitor, 2006, 2018b).

An alternative opinion was proposed by Pfeiffer (1997) who regards *Pseudodama* as a subgenus of *Dama*. This viewpoint is based mostly on minor details of the dental and postcranial morphology.

The first attempt to determine the phylogenetic relationships between European and Asian Plio-Pleistocene cervids was undertaken by Di Stefano and Petronio (2002). The Italian authors proposed several taxonomic changes and phylogenetic schemes that require a detailed analysis here:

i) The cited authors included *M. punjabiensis* in the genus *Axis* and regarded this species as a side branch of the *Axis shansius* – *Axis axis* lineage. The genus *Axis*, according to Di Stefano and Petronio (2002), includes also primitive fallow deer with four-pointed antlers, *Dama eurygonos*, and a primitive small-sized deer with four-pointed antlers, *Cervus nestii*. The conclusions of Di Stefano and Petronio (2002) are based on antler morphology, however, their arguments are not clearly articulated. *Dama eurygonos* is characterized by the typical antler bauplan for fallow deer with a very open angle of the first ramification, the presence of a trez tine, which is homologous to the anterior tine of the second ramification in *Metacervocerus* (according to the antler tine homology scheme developed by Beninde, 1937 and Korotkevich, 1988), and the distal portion of the beam (homologous with the posterior tine of the second ramification in *Metacervocerus*) supplemented with a crown tine set on the posterior side of the beam. Antlers and dentition of *D. eurygonos* provide even more characteristics specific to the genus *Dama*: the flexed and domed braincase, the large orbits, the relatively short orbitofrontal part of the antler, and short pedicles with a vertical insertion on the skull (Croitor, 2006). Antlers of *Cervus nestii* are characterized by a pearled surface and a different type of distal fork formed by two equal-sized tines

oriented rostrally as in *C. elaphus acoronatus*; one can call this morphological condition a terminal type of crown. According to Beninde (1937), the orientation of distal antler fork provides information about the evolutionary history of the antler and has taxonomic value. The second basal tine (bez tine) is missing. However, the cranial morphology shows a strong affinity with modern red deer: the braincase is barely flexed, the pedicles are relatively long and sloped backwards from the face, and the orbitofrontal part of skull is elongated (Croitor, 2006).

ii) *M. pardinensis*, *M. rhenanus*, and *M. perolensis* (often regarded as a junior synonym of *M. rhenanus*) are placed by Di Stefano and Petronio (2002) in the genus *Rusa*. The arguments for this taxonomic assignment are not clear. Unlike in *Rusa unicolor*, the antler surface in *M. pardinensis* and *M. rhenanus* is smooth, the basioccipital is broadened and bell-shaped, the orbitofrontal part of the cranium is short, and the upper canines are missing (this character is known for *M. rhenanus* only).

iii) Di Stefano and Petronio (2002) regard the lineage *M. rhenanus* - *M. perolensis* from the Early Pleistocene of Western Europe as a direct ancestor of the genus *Dama*. *Metacervocerus* shares with *Dama* the shape of basioccipital and the absence of upper canines. Some of the cranial features of *M. rhenanus* (the braincase flexion and the length and orientation of the pedicles) exhibit the primitive condition and do not contradict the hypothesized phylogenetic relationship with fallow deer. However, the braincase in *M. rhenanus* is relatively shorter than in fallow deer (Croitor, 2018b) and therefore represents an advanced character that rules out the possibility of a direct phylogenetic relationship between *M. rhenanus* (including *M. perolensis*) and the genus *Dama*. *M. rhenanus* shares with *D. dama* long nasal bones extended behind the anterior orbital line, however, this feature should be regarded as a parallelism, since the nasal bones in *D. eurygonos* are short (Croitor, 2006).

The cluster analysis in this study (Fig. 10) is based on available cranial, dental, and antler characteristics (Tab. 4) that are considered to be diagnostic characters at the genus and species levels (Vislobokova, 1990). Therefore, the obtained results should be regarded rather as an evaluation and confirmation of the systematic and taxonomic significance of the chosen available characters. Caution is suggested in applying the obtained cladogram to phylogenetic studies, first of all because some of the morphological characteristics could be unavailable and, secondly, the proposed cluster analysis includes only better known species.

The results of the analysis reveal interesting, but quite predictable relationships among the cervids of the subfamily Cervinae involved in this study. The cervid species compared form two main clusters: the red deer group including *Cervus nestii* (Azzaroli, 1947) from the Early Pleistocene of Upper Valdarno (Italy),

characterized by a narrow, wedge-shaped basioccipital, the presence of upper canines, and a pearled antler surface, and the *Axis-Metacervocerus-Dama* cluster characterized by a bell-shaped basioccipital, the loss of their canines, and a smooth antler surface.

M. punjabiensis is nested within the cluster of *Metacervocerus* together with *M. pardinensis*, *M. shansius*, and *M. rhenanus*, thus confirming the systematic and, apparently, phylogenetic unity of those cervid forms. This result supports the inclusion of *M. punjabiensis* in the genus *Metacervocerus* as was proposed earlier by Croitor and Stefaniak (2009).

The association of *Dama* with *Metacervocerus* is quite surprising and apparently based on the “adaptive” antler bauplan shared by *Dama* and *Metacervocerus*. The apomorphic long nasal bones shared by modern *D. dama* and *M. rhenanus* does not have decisive importance since the primitive fallow deer *D. eurygonos* is also clustered with *Metacervocerus*. The affinity identified between *Dama* and *Metacervocerus* requires further discussion. *Dama* is an endemic, quite specialized genus with a distribution restricted to the Euro-Mediterranean region that appeared in Europe during the Early Pleistocene and does not have any closely related counterparts from the paleontological record of Eastern Asia. “*Dama*” *sericus* Teilhart et Trassaert, 1937 is characterised by a completely different antler bauplan that is instead reminiscent of *Rucervus* (*Arvernoceros*): the tree tine is missing, the first ramification is very highly situated, the angle of the first ramification is acute, and the palmation is formed by posterior crown tines as in *R. (Arvernoceros) ardei* (Croitor, 2018a).

The earliest fallow deer, *D. eurygonos*, had already evolved all of the specialized cranial and dental features of modern fallow deer and is distinguished only by short nasal bones and missing distal palmation (Croitor, 2006). *Metacervocerus* marks its earliest appearance in Europe during Early Pliocene (Croitor and Stefaniak, 2009). *M. pardinensis* from the Pliocene of Europe is more advanced than its Asian counterparts in having relatively short pedicles, but shows similarities to *M. punjabiensis* in its dental morphology: the split lingual wall of P², the additional enamel fold of the protocone on the upper molars, and the inner hypoconal folding on the premolars (Heintz, 1970). The only morphological feature of the dentition that distinguishes *M. pardinensis* – the type species of the genus *Metacervocerus* – is the development of the lingual cingulum on the upper molars. It should be noted here that *Metacervocerus* sp. from the Early Villafranchian fauna of Montopoli, Italy is a roughly coeval cervid with *M. pardinensis* that lacks cinguli in its upper molars. It is not clear if the specimen from Montopoli represents a distinguishable taxon, or provides evidence that the development of cinguli is a variable character in *M. pardinensis*.

M. rhenanus from the Early Pleistocene of Europe is lacking the cingulum on the upper molars and is characterized by such advanced characters as long nasal bones (Croitor, 2006). Therefore we join the cautious opinion of Azzaroli (1992) that European *Metacervocerus* may belong together with *Dama* in the same stem group, although the paleontological evidence of the early evolution of this cervid stock is still missing.

The distant sister relationship between *Metacervocerus* and *Axis* suggested by our analysis is in accordance with the earlier results of Bai et al. (2017) based on antler morphology and Mennecart et al. (2017) based on bony labyrinth morphology. Generally, *Metacervocerus* shows a similarity to *Axis* in the degree of evolutionary specialization. The relative length of the splanchnocranium in *M. rhenanus* (55.1%, n=2) is very close to the mean value obtained for *A. axis* (54.9%, n=4), but also is close to the relative splanchnocranium length in *D. dama* (55.0%, n=13). *Metacervocerus* and *Axis* are characterized by similarly rounded and moderately large bullae tympani and (with exception of *M. punjabiensis*) by a similar relative length of the neurocranium (Croitor, 2014). The difference in the development of the second antler ramification suggests that *Metacervocerus* and *Axis* acquired three-pointed antlers independently and, thus, represent two different phyletic lineages that evolved from different two-pointed antler forerunners. Unlike *Axis*, *Metacervoceros* maintains primitive features of the upper cheek teeth, such as a relatively long premolar series.

M. punjabiensis is distinguished from *A. axis* by its primitive narrow and long braincase. Interestingly, this feature joins *M. punjabiensis* with *M. giganteus* and *D. dama* and is concordant with the results of our cluster analysis (Fig. 10). The close evolutionary relationship between *Dama* and *Megaloceros* was confirmed by genetic studies (Lister et al., 2004). One can assume that *M. punjabiensis* possesses the specific and possibly primitive proportions of the braincase that are found in the *Megaloceros-Dama* phylogenetic lineage. The peculiar shape of braincase of *M. punjabiensis* suggests that similarities between the braincase proportions of *A. axis* and *M. shansius* and *M. rhenanus* could be the result of evolutionary parallelism. The Late Tertiary of Eastern Asia has yielded a variety of cervines with three-pointed antlers, whose systematics and phylogenetic relationships are still not clear (Shikama, 1941; Teilhard de Chardin and Piveteau, 1930; Teilhard de Chardin and Trassaert, 1937). Possibly, future revisions of Late Tertiary plesiometacarpal deer from Eastern Asia will give answers to questions about the phylogenetic relationships among *Metacervocerus*, *Dama*, and other related forms.

The details of the cranial morphology discussed in this study helps to answer questions about the possible relationship of *M. punjabiensis* with a large *Metacervocerus* specimen from the Early

Pleistocene of Milcovu din Vale near Slatina (Romania). The cranial fragment Nr. 161 from Milcovu din Vale is an almost complete braincase with damaged frontal bones and the basal portions of the antlers. The Romanian specimen is quite large and approaches the size of *M. punjabiensis* and *M. shansius* (Tab. 1). The presence of long pedicles is another feature that may be regarded as shared by the deer from Milcovu din Vale and Asian *Metacervocerus* (Fig. 5). The braincase of Nr. 161 apparently belongs to a young adult individual and is characterized by rather long and divergent pedicles (the angle of divergence is 110°) situated in the frontal plane (sloped backwards) and a relatively broad braincase. The Romanian specimen is more similar to *M. shansius* in its relatively broad braincase (Fig. 4). However, the stronger divergence of the pedicles is an advanced morphological condition that distinguishes the deer from Milcovu din Vale from *M. shansius*.

5. Conclusions

The cluster analysis of dental, antler, and neurocranial characters confirms the attribution previously suggested by Croitor and Stefaniak (2009) of *Cervus punjabiensis* to the genus *Metacervocerus* Dietrich, 1938. The available diagnostic characteristics also confirm the validity of the genus *Metacervocerus* as separate from modern *Axis*. The cluster analysis of dental, cranial, and antler morphology of the Siwalik cervid under study supports the suggestions of Azzaroli (1954) and Bai et al. (2017) that *M. punjabiensis* and *M. shansius* have no direct phylogenetic relationship with modern *Axis axis*. *Metacervoceros* is characterized by a different origin of the second antler ramification, which is formed by an additional tine inserted on the anterior side of the beam, unlike *Axis* that forms its second ramification by adding an additional tine on the posterior side of the beam. Unlike *Axis*, *Metacervocerus* also maintains primitive proportions of the upper cheek tooth row, having a relatively long premolar series.

All species of *Metacervocerus* possess antlers that are of fairly similar shape, but they differ in their various combinations of advanced and primitive dental and cranial characters. Unlike *M. shansius* from the Late Tertiary of China, *M. punjabiensis* is characterized by an elongated and narrow braincase, a relatively broad occiput, a strong divergence of the pedicles, an accessory enamel fold of the protocone on the upper molars, and labiolingually broad upper cheek tooth crowns. The better known *M. rhenanus* from the Early Pleistocene of Western Europe shares with *M. shansius* the shape and proportions of the braincase and upper molars, but is more advanced in having relatively short and divergent pedicles. The large form of *Metacervocerus* from the Early Pleistocene of Milcovu din Vale (Olteț River Valley, Romania) is characterized by long, divergent pedicles and a relatively broad braincase, therefore exhibiting morphological and metric affinities with Asian *Metacervocerus shansius*.

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TABLES

Table 1. Cranial measurements of the type specimen of *Cervus punjabiensis* (AM) compared with *Metacervocerus* from Ceysaguet (CEY, Late Villafranchian, France), Milcovu din Vale (MCV, Early Pleistocene, Romania), and Montopoli (IGF, Early Villafranchian, Italy).

Variable	AM- 19911	CEY- 2318	CEY- 15194	CEY- 11217	IGF- 1408	MCV- 161
Length of the upper tooth row (P ² -M ³)	101.8	87.2	83.8		85.2	
Length of the upper molar series (M ¹ -M ³)	57.6	51.4	49.4		50.9	
Length of the upper premolar series (P ² -P ⁴)	43.3	39.2	37.0		37.8	
Occipital breadth	141.4			97.0	102.3	119.5
Occipital height	102.5			66.7	65.9	
Breadth of the occipital condyles	84.0			58.0	51.2	64.3
Frontal breadth	87.3	98.8	104.6	103.1	91.2	
Breadth of the neurocranium	77.3	82.8	82.2	77.7		86.3
Breadth of the nasal bones	27.5					
Distance between bregma and inion	95.6	79.5		74.3	81.0	84.0
Breadth of the foramen magnum	33.4					

Table 2. Pedicle and antler base measurements (millimeters) of the type specimen (left side) of *Metacervocerus punjabiensis*.

site	collection number	H pedicle	DAP pedicle	DLM pedicle	DAP above burr	DLM above burr	H ram.
Chandigarh, Siwaliks	AM-19911	51.1	28.4	30.8	37.8	34.5	51.9

Table 3. Tooth crown measurements of the type specimen of *Metacervocerus punjabiensis*, AM-19911.

Tooth	Length	Breadth
P ² right	15.6	13.6
P ³ right	15.2	17.8
P ⁴ right	13.4	17.6
M ¹ right	18.1	19.7
M ³ left	21.5	20.2

Table 4. Craniodental characteristics used in the hierarchical clustering. The data matrix includes also mesodonty reported by Brown (1926) for *Metacervocerus punjabiensis*. Abbreviations: Mpj, *Metacervocerus punjabiensis*; Mpr, *Metacervocerus pardinensis*; Mrn, *Metacervocerus rhenanus*; Mss, *Metacervocerus shansius*; Aax, *Axis axis*; Rur, *Rusa unicolor*; Rts, *Rusa timorensis*; Ddm, *Dama dama*; Deg, *Dama eurygonos*; Ces, *Cervus elaphus*; Cni, *Cervus nestii*.

	basioccipitale	upper canines	pedicle length	pedicle position	pedicle divergence	terminal crown	posterior crown	antler pearling	nasale length	cingulum	protoconal fold	1-st ramification	mesodonty	orbitofrontal part	Flexed braincase	antler type	bez tine
Mpj	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0
Mpr	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0
Mrn	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0
Mss	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0
Aax	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rur	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Rts	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	1	0
Ddm	1	0	1	1	1	0	1	0	1	0	0	0	0	0	1	1	0
Deg	1	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1	0
Ces	0	1	1	0	1	1	0	1	0	0	0	0	0	1	0	1	1
Cni	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0

FIGURE CAPTIONS

Figure 1. Frontal view of the holotype AM-19911 of *Metacervocerus punjabiensis* (Brown, 1926). Most of splanchnocranium of the type specimen is reconstructed.

Figure 2. Median view of the right (A) and left (B) antlers of the holotype AM-19911 of *Metacervocerus punjabiensis* (Brown, 1926).

Figure 3. The holotype AM-19911 of *Metacervocerus punjabiensis* (Brown, 1926): A, occipital view; B, parietal view; C, ventral view.

Figure 4. Braincase measurements of *Metacervocerus punjabiensis* compared to modern and fossil cervid species: A, braincase breadth behind pedicles; B, distance between bregma and inion. Data on *M. shansius* are derived from Teilhard de Chardin and Trassaert (1937).

Figure 5. Pedicle measurements of *Metacervocerus punjabiensis* compared to species and forms of *Metacervocerus* (mean values and standard deviations). Data on *M. shansius* are derived from Teilhard de Chardin and Trassaert (1937); data on *M. pardinensis* are derived from Heintz (1970); data on *M. rhenanus* are derived from Spaan (1992).

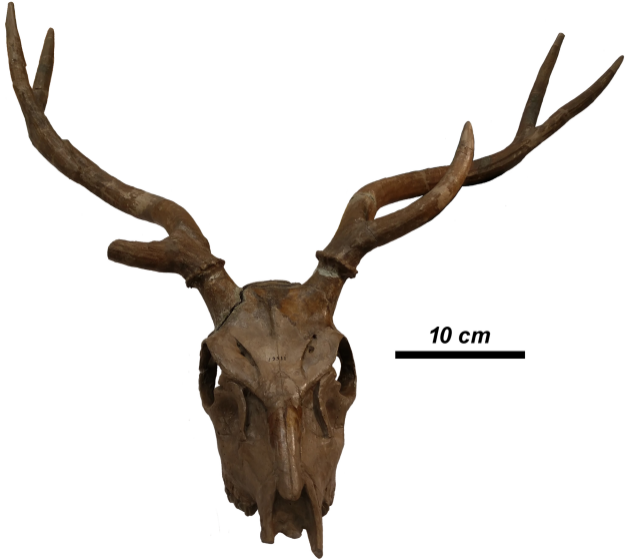
Figure 6. Upper tooth series proportion and length of *Metacervocerus punjabiensis* compared to modern and fossil cervines (mean values and standard deviations). Data on *M. shansius* are derived from Teilhard de Chardin and Trassaert (1937); data on *M. rhenanus* are derived from Spaan (1992) and Boeuf et al. (1992).

Figure 7. Upper premolar crown measurements (length and breadth, in millimeters) of *Metacervocerus punjabiensis* compared to fossil Villafranchian deer (mean values and standard deviations). Data on *M. shansius* are derived from Teilhard de Chardin and Trassaert (1937); data on *M. rhenanus* and *P. perrieri* are derived from Heintz (1970).

Figure 8. Upper molar crown measurements (length and breadth, in millimeters) of *Metacervocerus punjabiensis* compared to fossil Villafranchian deer (mean values and standard deviations). Data on *M. shansius* are derived from Teilhard de Chardin and Trassaert (1937); data on *M. rhenanus* and *P. perrieri* are derived from Heintz (1970).

Figure 9. Antler size of the type specimen of *Metacervocerus punjabiensis* compared to fossil and modern cervines (mean values and absolute measurement range, in millimeters): A, antler length, B, antler circumference above the first tine. Data on *M. shansius* are derived from Teilhard de Chardin and Trassaert (1937); a part of the data for *M. rhenanus* are derived from Spaan (1992) and Boeuf et al. (1992); a part of data for *A. axis* are derived from Ward (1892). The estimated antler beam circumferences for *M. shansius* and *M. rhenanus* are based on the anteroposterior diameter of the antler above the burr.

Figure 10. Cluster analysis of the diagnostic cranial, dental, and antler characters of *Metacervocerus punjabiensis* and selected modern and fossil cervid species from the Oriental Zoogeographic Realm and Western Palearctic, including the so-called “*Dama*-like deer” (*M. pardinensis*, *M. rhenanus*, *D. eurygonos*, *C. nestii*). The cophenetic correlation coefficient is 0.9152.



10 cm





A



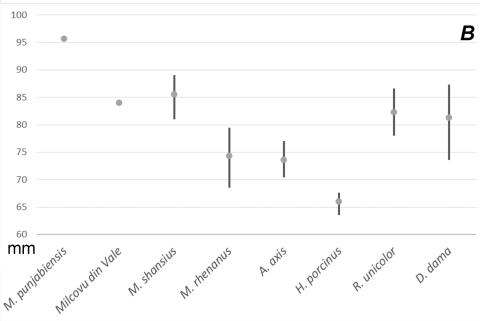
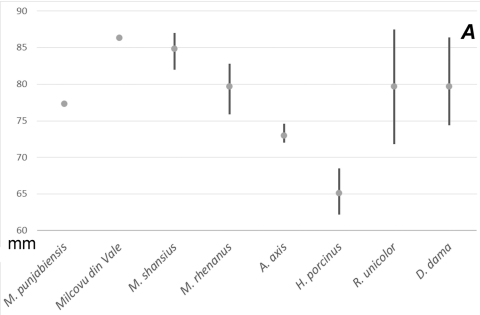
B

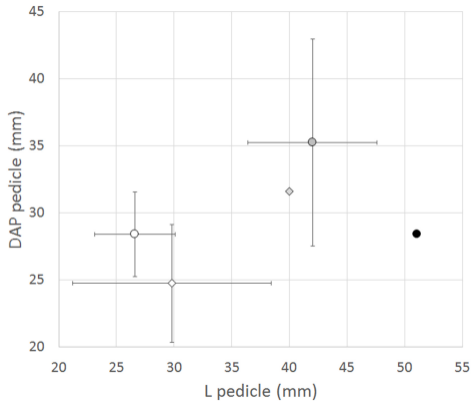


C

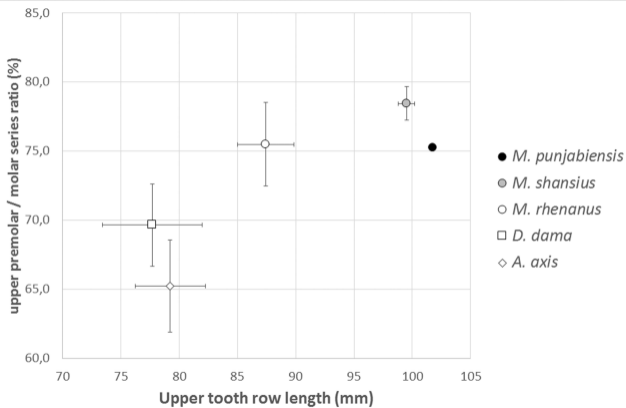
5 cm

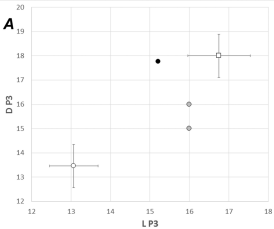






- *M. punjabiensis*
- *M. shansius*
- *M. pardinensis*
- ◇ *M. rhenanus*
- ◇ *Milcovu din Vale*



A**B**