Systematical position and paleoecology of the endemic deer *Megaceroides algericus* Lydekker, 1890 (Cervidae, Mammalia) from the late Pleistocene-early Holocene of North Africa ✿

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Abstract

The unusual cranial morphology of the endemic extinct African deer *Megaceroides algericus* (Lydekker, 1890) is described. Some details of cranial and dental morphology suggest that *M. algericus* is closely related to the Eurasian giant deer *Megaloceros giganteus* (Blumenbach, 1799). The paper presents also a discussion on paleoecology and functional morphology of *Megaceroides algericus*, as well as its origin, phylogenetic and taxonomic position. *Megaloceros mugarensis* (di Stefano, 1996) from the middle Pleistocene of Levant is regarded as a probable forerunner of *Megaceroides algericus*.

1. Introduction.

Cervidae represents a successful family of ruminants that arose in the mid-Tertiary period in Eurasian tropics. However, because of its specific evolutionary and ecological strategy, this species-rich i and ecologically diversified family, apart from a few exceptions, failed to colonize the African continent. According to Geist (1998), cervids with their low forage habit specialization are poor food competitors in mature and species-rich ecosystems with respect to other groups of herbivores such as bovids and equids, amongst other coevolved ecological specialists. Ecologically opportunistic cervids are most successful in young ecosystems with large amplitude of environmental fluctuations (Geist, 1998). Indeed, the paleontological record and modern fauna give only two examples of successful evolutionary survival of cervids on the African continent: *Megaceroides algericus* (Lydekker, 1890) and *Cervus elaphus barbarus* Bennet, 1833 (Gentry, 2010).

The origin and systematic position of the North African fossil deer *Megaceroides algericus* is a subject to debates and contradictions in the scientific literature for more than a century. The extinct species *M. algericus* represents the exceptional zoogeographic instance of an endemic and extremely specialized form of deer that evolved on the African continent. The second African cervid, *Cervus elaphus barbarus*, is a primitive, small-sized subspecies of red deer which survived until the present days and does not show unusual or particular evolutionary specializations, possibly with exception of some pedomorphic traits (Geist, 1998). The isolated and highly restricted North African distribution of *M. algericus* represents an interesting but still poorly understood evolutionary and paleozoogeographic case. The present article proposes a taxonomic, morphological, morpho-functional, paleobiological, and phylogenetic study of the "thick-jawed deer" *M. algericus* that aims to contribute to the better understanding of this rare zoogeographic instance of endemic North African cervid.

2. Historical background

The first description of the species belongs to Lydekker (1890). He described a maxilla with an upper tooth series comprising P^4-M^3 of a medium-sized deer from Hammam Mescoutine (Algeria) as *Cervus algericus*, noting a strongly developed cingulum, and assumed a possible phylogenetic relationship of the new species with the giant deer *Megaloceros giganteus*. Somewhat later, Pomel (1892) created another species, *Cervus pachygenys*, which was based on a very pachyostotic and quite bizarre ("pathological", according to Pomel, 1893) lower mandible from the Neolithic of Algeria. The sample described by Pomel (1893) also included an isolated upper molar without lingual cingulum.

Joleaud (1914, 1916) brought together in synonymy Lydekker's and Pomel's species and stressed the affinity between the African deer and the European giant deer, assuming for the African form an intermediate position between *Megaloceros* and *Dama*. Joleaud (1914, 1916) placed the North African deer in his new subgenus *Megaceroides* within the genus *Cervus* in order to underline its assumed archaic character and transitional systematic position. Arambourg (1932, 1938) elevated *Megaceroides* to the genus level and reported on some new important findings of cranial remains of *Megaceroides algericus* from Algeria (Guyotville) and Morocco (Ain Tit Mellil). Arambourg (1938) provided figures of those findings, but did not describe them in details.

The studies of Italian researchers published in the second half of the XXth century gave a new impetus to the debates on taxonomy and systematic position of the endemic African cervid. Azzaroli (1953) proposed a new evolutionary and systematic model for the genus *Megaloceros*, which included all giant and some smaller plesiometacarpal Old World cervids, including presumed late Pleistocene descendant dwarfed forms from Mediterranean islands and *Megaceroides algericus*. Azzaroli (1953) divided the genus *Megaloceros* Brookes, 1828 (the genus name *Megaceros* Owen, 1843 was applied in the cited work) into two informal evolutionary branches called the "*giganteus* group" and the "*verticornis* group" after the best known species representing each stock. *Megaceroides algericus*, according to this author, is a terminal form of the "*verticornis* group" showing signs of evolutionary "degeneration", such as a small body size, the extreme degree of hyperostosis, and a very marked shortening of the muzzle. Azzaroli (1953: p. 48) recognized that the relationships of *M. algericus* with European forms are not clear, therefore he avoided using the name *Megaceroides* in his evolutionary model of giant deer. Nonetheless, Azzaroli (1953) indicated some morphological characters of *Megaceroides algericus*, such as the flattened shape of the frontlet and traits of "stunting" in the antler morphology and overall size, which permitted him to include the North African cervid in his "*verticornis* group". He noticed that *M. algericus* coincides in some features with *Sinomegaceros pachyosteus* (placed by Azzaroli, 1953 in the "*giganteus* group") in its smaller body size, the extreme degree of hyperostosis, and the shortening of the muzzle. Ambrossetti (1967) accepted Azzaroli's opinion and placed all "*verticornis*-like" deer from Europe together with the Algerian endemic deer in the subgenus *Megaceros* (*Megaceroides*). Later, Azzaroli and Mazza (1993) elevated *Megaceroides* to the generic rank. Later on, Azzaroli's (1953) suggestion on the morphological affinity between *Megaloceros algericus* and *Sinomegaceros pachyosteus* was supported by Thomas (1979) and Hadjouis (1990).

Finally, Azzaroli (1979, 1994) assumed that *Megaceroides algericus* and *Praemegaceros dawkinsi* (= *Megaceroides dawkinsi* according to Azzaroli, 1979) resulted from a similar evolutionary dwarfing process caused by geographical isolation in unfavorable conditions. The flat shape of the frontal bones, the similarly diminished body size, and the disproportionately thin antler beams with respect to relatively large antler burrs and robust pedicles are regarded as stunting traits shared by *M. algericus* and *P. dawkinsi* (Azzaroli and Mazza, 1993).

Kahlke (1965) proposed the old genus name *Praemegaceros* Portis, 1920 (substituting the genus name *Orthogonoceros* Kahlke, 1956 with type species *Cervus verticornis* Dawkins, 1872) for European deer of the "*verticornis* group", thus disregarding Azzaroli's (1979) suggestion of a close phylogenetic relationship between *Megaceroides algericus* and the "*verticornis* group". Two years later, Radulesco and Samson (1967) published a detailed taxonomical study of Pleistocene large-sized deer and confirmed the validity of the genus name *Praemegaceros* for the "*verticornis* group", acting as first revisers. The endemic British deer *Cervus dawkinsi* Newton, 1882 was designated as the type species of the genus *Praemegaceros* (Radulesco and Samson, 1967).

From that point, debates on the taxonomy of large-sized deer from Pleistocene of Western Palearctic became very confusing, since the disputed genera *Praemegaceros* and *Megaceroides* were typified by the poorly known endemic and morphologically odd species *Praemegaceros dawkinsi* and *Megaceroides algericus*. Vislobokova (2012a: p. 687, 2012b: p. 58; 2013: p. 911) regards *Cervus verticornis* Dawkins, 1872 as the type species of *Praemegaceros* and granted to Kahlke (1965) the title of first reviewer of the genus. Nonetheless, Vislobokova (2012b: p. 61; 2013: p. 913) also proposes *Cervus dawkinsi* as the type species of the nominotypical subgenus *Praemegaceros* (*Praemegaceros*). It is necessary to keep in mind that *Praemegaceros* Portis, 1920 was originally based on *Cervus dawkinsi*, while *Cervus verticornis* together with *Cervus savini* Dawkins, 1887 and *Cervus falconeri* Dawkins, 1868 were included in *Praedama* Portis, 1920 (Portis, 1920; Radulesco and Samson, 1967; Azzaroli, 1979) and, therefore, cannot be used as type species for *Praemegaceros* – according to Article 44 of the ICZN, a genus and its nominotypical subgenus are denoted by the same type species.

Hadjouis (1990) regarded *Megaceroides* as a subgenus of *Megaceros* Owen, and proposed an improved diagnosis for *Megaceroides* and a synonymy list of *M. algericus*. In opinion of Hadjouis (1990), the morphology of the dentition (first of all, the strongly developed cingulum on upper molars) and the extremely strong mandibular pachyostosis make *M. algericus* somewhat similar to the Asian large-sized deer *Sinomegaceros*

pachyosteus, once again supporting the Azzaroli's (1953) previous observation. The missing posterior tine in antlers of *M. algericus* was regarded by Hadjouis (1990) as one of the most important characters distinguishing the African endemic deer from the European giant deer. Nonetheless, this viewpoint has been contested by Azzaroli and Mazza (1993) and Azzaroli (1994), who questioned the taxonomical value of the cingulum in upper molars and the mandibular pachyostosis, which, according to the Italian authors, are quite variable in large-sized deer.

Abbazzi (2004) pointed out the resemblance of the neurocranium shape of *Megaceroides algericus* with *Praemegaceros solilhacus* (Robert, 1829) and *P. dawkinsi*, however, she did not discuss the phylogenetic position of *M. algericus* and, following the opinion of Hadjouis (1990), she restricted *Megaceroides* to the type species. Gentry (2010) included *Megaceroides* into the synonymy of *Megaloceros*.

Vislobokova (2009, 2012a, 2012b, 2013) includes *Megaceroides* in the tribe Megacerini Viret, 1961, that contains a large number of continental and insular late Miocene-Pleistocene cervids presumably closely related to the genera *Megaloceros* and *Praemegaceros*. Vislobokova (2012b, 2013) suggests that *Megaceroides* is a monotypic taxon that includes a single peculiar cervid form closely related to European *Praemegaceros* and possibly may be included in the latter genus as a subgenus in the case its belonging to *Praemegaceros* will be demonstrated. Vislobokova (2012b, 2013) also regards Azzaroli's informal *verticornis*-group and *giganteus*-group as subtribes Praemegacerina and Megacerina within the tribe Megacerini. Since the phylogenetic relationships among the so-called "giant deer" (including also some smaller continental forms and insular dwarfs) are not well founded (Croitor, 2006), the new taxonomical units proposed by Vislobokova most probably are polyphyletic.

The taxonomical revision of the genus *Praemegaceros* and a preliminary account on the systematic position, morphology, and paleoecology of *Megaceroides algericus* were already published in previous reports (Croitor, 2004, 2006, 2014; Croitor and Bonifay, 2001; Croitor and Kostopoulos, 2004; Croitor and al., 2006). We pointed out that the morphology of the dentition (the presence of the cingulum in upper molars, the relatively short lower premolar series, and the brachyodonty) make the Algerian deer close to *Megaloceros giganteus* from moderate latitudes of Central and Western Eurasia (Croitor and Bonifay, 2001). Therefore, we adjoined the opinion of Radulesco and Samson (1967) on the validity of the genus name *Praemegaceros* for the "*verticornis* group". Later on, a direct phyletic relationship between the dwarfed middle Pleistocene *Praemegaceros dawkinsi* and larger early Pleistocene *Praemegaceros obscurus* was suggested (Croitor, 2006). This point of view

is supported, *inter alia*, by the presence of vestigial basal antler tines in *P. dawkinsi*, which are homologous with long and strong basal tines in *P. obscurus*.

Regarding the size and proportions of the braincase from Ain Tit Mellil discovered by Arambourg (1938) and the pachyostotic mandibles from various North African sites, I pointed out the disproportion between the relatively broad and large braincase and the short and weak anterior part of the mandibles, presuming the mixed character of the material ascribed to *Megaceroides algericus* and, therefore, I proposed to exclude the African material from the taxonomical debates of European large-sized cervid forms (Croitor, 2004). Later, I had the opportunity to study the complete skull of *Megaceroides algericus* from Guyotville (figured by Arambourg, 1932) that represents a poorly understood and aberrant morphological specialization for Cervidae (Croitor, 2006). In my previous publication, only a general description and some measurements of the cranial and mandibular material of *M. algericus* were published; however, even that brief overview provided arguments against its use as the type species for giant and dwarfed deer arbitrarily placed in the "*verticornis* group" and now included in the genus *Praemegaceros* (Croitor, 2006, 2014).

Despite of the available fine cranial and dental material, antlers and postcranial bones of *Megaceroides algericus* remain little known. Pomel (1893) described and figured a damaged, but obviously very robust and relatively short cervid radius from Berrouaghia (Algeria) characterized by a comparatively broad bone shaft (the mid-shaft measurement amounts to 40 mm, exceeding the analogous measurement for *Megaloceros giganteus*) and two fragments of slightly compressed from the sides (latero-medially) antler tines. Hadjouis (1990) described several shed antlers of *Megaceroides algericus* from Phacocheres (Algeria) with the missing distal part of palmation and the anterior (middle) tine, as well as a fragment of a narrow distal palmation. These specific although very incomplete data on the antler and postcranial morphology of *Megaceroides algericus* suggest peculiar eco-morphological adaptations, but practically do not contribute to the understanding of the paleoecology and evolution of this species.

Nonetheless, despite of long lasting debates on its systematic position and phylogenetic relationships, even the fine available cranial material of *Megaceroides algericus* remains rather superficially described. In the present paper, a detailed morphological description of the cranial remains and dentition of *Megaceroides algericus*, as well as a discussion on its paleoecology and phylogenetic relationships are therefore provided.

3. Material and methods.

The described fossil material comes from the old historical collections stored in the National Museum of Natural History in Paris. All fossil remains were found in archaeological Paleolithic sites; however, their exact stratigraphic origin and absolute age remain unclear. Nonetheless, the detailed morphological description of the material included in this study was never published before and represent a significant information gap that impede the advance of our knowledge of taxonomy, systematics and phylogeny of Eurasian large sized and endemic Mediterranean deer. The studied material (Table 1) comes from the following sites (Fig. 1):

- **Guyotville** (= Ain-Benian: Hadjouis, 1990; = Anglade: Fernandez et al., 2015; = Sintès: Camps, 1992), Algeria. The local fauna from Guyotville, associated with a Mousterian industry, was characterized by Arambourg (1935) as a middle Paleolithic assemblage due to the presence of *Rhinoceros mercki* and *Hippopotamus amphibius*. The better preserved antlered skull (distal portions of antlers are not preserved; no collection number) from Guyotville was excavated and briefly described by Arambourg (Arambourg, 1932: fig. 3) and has been mentioned by Azzaroli and Mazza (1993) with regard to its forehead shape. Hadjouis (1990) quotes briefly some cranial characters based on the specimen from Guyotville and published measurements of its dentition. Only an approximate condylo-basal length of this skull could be measured (Croitor, 2006), since its occipital condyles and foramen magnum were destroyed, apparently, by ancient hunters who extracted the brain tissue from the braincase. The sample from Guyotville includes also two hemi-mandibles (Nr. 336, Nr. 337, "Collection of Arambourg") which remained unpublished;

- **Ain Tit Mellil** (= Tit Mellil: Vaufrey, 1955), Morocco. The exact stratigraphic origin of the fossil remains is unknown and they age was generally assumed as "the beginning of Würm glaciation" (Vaufrey, 1955). The braincase MOC148 from Ain Tit Mellil (figured in Arambourg, 1938: pl. II, fig. 2) was briefly discussed by Abbazzi (2004: fig. 6) and Vislobokova (2013: fig. 56a, b);

- **Grotte de la Madeleine** (= Taza 1: Fernandez et al., 2015), Algeria. The Paleolithic site of Taza 1 includes three layers dated from >39,000 to 13,800 ± 130 y. BP (uncalibrated age; Medig et al., 2005). Therefore, a late Pleistocene age is assumed for historical collection of fossils yielded by this site (Fernandez et al., 2015). The studied material includes two fragmented mandibles: the well preserved right hemimandible figured in Croitor (2006: fig. 2A-B; no collection number) and another specimen with a malformation in the area of the processus angularis (no collection number). The museum label provides the following information: "*Cervus algericus* – figuré: Pl. IV, Fig. 4",; however, this label does not contain any bibliographic information;

- Filfila, Algeria. A Würmian age was assumed for the fauna from Filfila (Ginsburg et al., 1968). The sample of *Megaceroides algericus* from Filfila (Thomas, 1979) includes a fragment of a right upper jaw (FIL169) with M^2 and M^3 and three hemi-mandibles (FIL166, FIL167, and juvenile FIL160). Only the best preserved specimen FIL166 was figured by Thomas (1979) and Abbazzi (2004: fig. 7).

The specific character of fossil material (fragmentary skeletal remains, limited number of fossils) restricted the choice of methodological approach. The safest estimation of cranial and dental morphological characters of *Megaceroides* was made possible by involving of few "typical" evolutionary and ecological cervid forms such as *Dama dama* (apparently, one of the closest species to *Megaceroides*, which maintains generalized cervid cranial morphology), *Megaloceros giganteus* (a giant species characterized by pachyostosis as *Megaceroides algericus*), *Muntiacus muntjak* (a tropical forest dweller, which possibly maintain the basic cranial morphology and proportions for Cervinae), and *Hydropotes inermis*, which belongs to the subfamily Capreolinae but represents a rare cervid example of ecological specialization connected to the periaquatic ecological niche). The material for craniological comparisons includes a series of skulls and mandibles of the modern fallow deer *Dama dama*, *Muntiacus muntjak*, and *Hydropotes inermis* stored in the osteological collections of the Zoological Museum "La Specola" (ZMS, Florence, Italy) and in the Natural History Museum of London (NHML), red deer *Cervus elaphus* stored in the zoological collections of the National Museum of Natural History in Paris (NMNH), and *Megaloceros giganteus* from various late Pleistocene sites of Ireland (NHML). The main measurements of the comparative material are presented in Tables 2 and 3. The statistical processing of data was not possible because of the restricted number of fossil material, but also because of quality and mixed character of the available comparative osteological material: the cranial material of some species (*M. muntjak* and *H. inermis*) was not abundant, and besides that, many specimens were obtained from parks, zoological gardens, and did not represent natural populations, together making the statistical processing of data became meaningless. Therefore, a single male skull of each species was selected for the comparative study.

The lengths of dental series are taken at the crown bases or at alveoli. The length of tooth crown is taken as a maximal measurable value. The length of tooth crown in upper cheek teeth is measured at the labial side of grinding surface. The breadth of tooth crown is measured at crown base. The terminology of dental morphology is adapted from Heintz (1971). The methodology of cranial measurements is adapted from Vislobokova (1990). The terminology of antler tines follows the homology of tines according to Azzaroli and Mazza

(1993) and Croitor (2006). The body mass estimation used here is based on dental variables according to Janis (1990).

Abbreviations: PP, premolar series; MM, molar series; L, length; H, height; D, width/breadth.

4. Systematic paleontology

Class Mammalia Linnae, 1758

Order Artiodactyla Owen, 1841

Sub-Order Ruminantia Scopoli, 1777

Family Cervidae Goldfuss, 1820

Subfamily Cervinae Goldfuss, 1820

Genus *Megaceroides* Joleaud, 1914

Megaceroides algericus (Lydekker, 1890)

1890. *Cervus algericus* sp. nov. - Lydekker, p. 602, fig. 1.

1892. *Cervus pachygenys* sp. nov. - Pomel, p. 213.

1893. *Cervus pachygenys* (Pomel) - Pomel, p. 35, pl. VII, figs. 1-7, pl. VIII, figs. 1-4.

1914. *Cervus* (*Megaceroides*) *algericus* Lydekker - Joleaud, p. 737.

1938. *Megaceroides algericus* (Lydekker) - Arambourg, p. 33, fig. 8.

1953. *Megaceros algericus* (Lydekker) - Azzaroli, p. 47, p. 51.

1967. *Megaceros* (*Megaceroides*) *algericus* (Lydekker) - Ambrosetti, p. 272.

1990. *Megaceros* (*Megaceroides*) *algericus* (Lydekker) - Hadjiouis, p. 249, figs. 1-4.

2010. *Megaloceros algericus* (Lydekker) - Gentry, p. 813.

Holotype: Left maxilla with P^3-M^3 (Lydekker, 1890: figured on p. 602), P^2 being completely destroyed and M^2 and M^3 being damaged; the cast is stored at the Natural History Museum of London (Lydekker, 1890: p. 604), collection number M10647 (Gentry, 2010). The length of the upper molar series M^1-M^3 amounts to 58.5 mm (measured from the figure). The location of the original fossil specimen is unknown. The holotype is characterized by the strong development of a basal enamel cingulum in the upper molars.

Type locality and horizon: Late Pleistocene from Hammam Meskoutin, Guelma (Algeria).

Occurrence: Late Pleistocene to Holocene (*ca*. 24,000 to 6641-6009 yr. BP; Fernandez et al., 2015).

Original diagnosis (Lydekker, 1890: p. 603): Somewhat smaller than *Cervus cashmirianus*, with brachyodont molars, having a very large inner cingulum, and the external surface complicated by the excessive development and reflection of the lateral ridges of the outer crescents so as to form distinct pockets on this surface at the base of the ridges in question.

Emended diagnosis (this work): A cervid species of medium size, slightly larger than modern fallow deer and smaller than red deer. The skull is very broad: the skull breadth attains more than 60% of the condylobasal length. Splanchnocranium is relatively short: the length measured from the anterior edge of the orbits to the prosthion is shorter than 1/2 of the condylobasal length. Skull bones with exception of zygomatic arches are very thick. Braincase is moderately flexed: the angle between parietal bones and face profile amounts to *ca*. 135°; parietal bones are flat. Pedicles are moderately long (their length approximately equals to their transversal diameter), deflected sideward and somewhat backward. Frontal bones are flat and very broad. Orbits are comparatively large; their anterior edges lay at the level between M^1 and M^2. Ethmoidal vacuities are completely closed. Preorbital fossae are not developed. The basioccipital is broad and bell-shaped. Upper canines are missing. The cingulum in upper molars is variable: it may be well developed, or almost completely missing. P_4 is molarized; its metaconid is fused with the paraconid. Mandible is very pachyostosic, with a low anterior part. The transversal section of the anterior portion of the hemi-mandible is circular. Antlers terminate with a palmation. The proximal part of antler beam has a circular transversal section and lacks basal tines. The tine inserted on the anterior side of the beam (homologous with the middle tine in *Megaloceros giganteus*) is situated from the burr at a distance exceeding *ca*. two times the diameter of antler base.

Description:

Skull. The cranium from Guyotville belongs to a rather aged individual with completely obliterated sutures and a deeply worn upper dentition (Figs. 2, 3). The area of left eye socket is damaged. The basioccipital part and anterior part of the premaxillary bones are destroyed, so the condylobasal length and some other measurements of the skull are given with approximation (Table 4). The overall shape of the cranium is atypical. The relatively short and very broad skull of *Megaceroides algericus* is unique among fossil and living cervids (Fig. 2). Interestingly enough, the length proportions of the cranium are modified insignificantly: the eye sockets are in normal position for a deer of such a size, the relative length of facial part before eye sockets is the shortest among deer involved in comparison (even somewhat shorter than in the insular dwarf *Praemegaceros cazioti*); however, the difference is not significant (Fig. 4) and the length proportions may be regarded as normal for a deer of this size in the subfamily Cervinae. The position of *bregma* between the posterior edges of pedicles and the position of *nasion* slightly caudally with respect to anterior edges of eye sockets are similar to the morphological condition found in *Megaloceros giganteus*. The orbito-frontal portion of the cranium is rather short, as in *Dama* and *Megaloceros*: the anterior edge of orbit is situated above the M^2-M^3 border. The eye sockets are relatively large, as in

Dama. The relative length of the upper tooth row with respect to basal length of skull amounts to 29.5%, fairly close to the ratio found in *Megaloceros*, *Axis* and *Dama*. Nonetheless, the position of upper cheek tooth row shifted toward the anterior represents a specific character of *M. algericus* (Fig. 5). The anterior displacement of the upper tooth row in *Megaceroides algericus*, apparently, resulted from the strong reduction of the predental length of the skull (distance between P^2 and prosthion). The parietal bones are flat. The face profile is straight. The braincase of *Megaceroides algericus* may be considered as rather flexed: the angle between the parietal plane and the facial profile amounts to 135° and shows an intermediate condition between *Dama* and *Megaloceros* (Fig. 6).

The cranial bones are very thick, reminding the cranial hyperostosis described in *Megaloceros*. However, unlike in *Megaloceros*, the vomer apparently is not affected by hyperossification (Fig. 3). The zygomatic arches are markedly thin and feeble, contrasting with the overall robustness of the skull.

The pedicles are rather long, set obliquely on the skull and somewhat deflected toward the rear and the sides. The pedicles are slightly compressed in the antero-posterior direction, however this compression is not as strong as in advanced species of *Praemegaceros* (*P. verticornis*, *P. dawkinsi*, and *P. solilhacus*). The frontal bones are very broad (corresponding to the disproportionally broad skull), flat and slightly depressed from both sides of the frontal suture. The ethmoidal orifices are completely closed. The preorbital fossae are not developed. The nasal bones are relatively narrow and rather long, extending behind the imaginary line connecting the anterior edges of orbits, as in *Megaloceros* and *Dama dama* (but not as in *Dama clactoniana* and early Pleistocene species of *Dama*; Croitor, 2014).

The area for the *musculus masseter* attachment on the upper maxilla is situated above the anterior edge of M^1 and posterior edge of P^4. The predental portion of the skull (anterior parts of maxillae and praemaxillary bones) is very broad and relatively short.

The braincase MOC148 from Ain Tit Mellil is similar in morphology and proportions to the previous specimen, but is characterized by slightly smaller size and by a more convex profile of the forehead (Figs. 7(A), 8). The basioccipital bone in MOC148 is broad and bell-shaped (Fig. 7(B)), with a transversal extension in the area of the pharyngial tubercles (the tubercles for the attachment of the *Musculus rectus capitus ventralis major*). The breadth of the basioccipital at tubercles amounts to 52.1 mm. The preserved left *bulla tympani* is rather large, rounded, projecting outside (as in *Dama*), compressed in the medio-lateral direction, with the following dimensions: 35.0 × 20.1 mm. The anterior bony thorn of *bulla tympani* is not present in *Megaceroides*, unlike some Cervinae (*Cervus*, *Rucervus*). The *foramina ovale* are comparatively small, with irregular shape approaching to a triangular outline. The

dimensions of *foramina ovale* are 6.6 × 6.0 mm (sin.) and 7.0 × 5.4 mm (dex.). The nasal bones are extended behind the line connecting the anterior edges of orbits (Fig. 9).

I did not have the opportunity to make a direct comparison of crania of *Megaceroides algericus* and *Sinomegaceros pachyosteus* from China; nonetheless, it is useful to compare at least the general shape of *M. algericus* with skull of *Sinomegaceros* from Choukoutien figured by Young (1932). It seems that the skull of *S. pachyosteus* is broadest at the level of orbits, reminding *M. algericus*, though its broadening is not so extreme as in the African deer. One can notice that the skull is broadest in *S. pachyosteus* at the posterior edge of the orbits, while the skull of *M. algericus* is broadest at the anterior edge of the orbits. This difference is conditioned, apparently, by the orientation of orbits, which are more forward-oriented in *S. pachyosteus*. One can assume that the noticed difference of orbit orientation represents an adaptation to forested environment in *S. pachyosteus*. Therefore, the side orientation of orbits in *M. algericus* should be regarded as a specific adaptation for open landscape in hoofed mammals allowing a wider field of view in order to escape approaching predators. *M. algericus* is characterized by a somewhat more flexed braincase than *S. pachyosteus* (the angle between the parietal plane and face profile line measured from the specimen figured by Young (1932) amounts to *ca.* 145°); both cervids are more advanced in this character than *M. giganteus*, which is characterized by a weak flexion of the braincase (see Vislobokova, 1990 for progressive change of this character in Cervidae). *S. pachyosteus* shows a different position of its orbit with respect of upper tooth row: according to the figure of Young (1932), the anterior edge of orbit is situated above the anterior part of M^2 (not above M^2-M^3 border as in *M. algericus*). Possibly, this difference is caused by relatively diminished size of teeth in *M. algericus* and their oral "migration".

Upper teeth. The anterior part of the maxillae is preserved and show that there were no canines (their alveoli are not present) in the specimen from Guyotville. Cheek teeth are relatively small (Table 5). The relative size of upper third molar is noticeably reduced, making M^2 larger than M^3. Only a moderately developed entostyle is present on the lingual side of the upper molars. The entostyle of the upper molars is flattened and well-expressed in the studied additional material. It may extend and partially edge with the lingual base of tooth crown; however a continuous (antero-linguo-posterior) large cingulum is not developed. There are no hypoconal spur and other enamel folds on upper molars. The lingual side of the P^4 is not split into protocone and hypocone, not even grooved. The lingual side of P^4 is bordered with a weak cingulum-like enamel fold.

The fragment of a maxilla with M^2-M^3 FIL-169 belongs to an older individual as indicated by the advanced stage of tooth crown wear (Fig. 10). The angle between labial and

lingual walls of upper molars (Fig. 10) amounts to 37º, as in *Dama dama*. The hypoconal fold is present only in M^3. Two small enamel folds are found on the external side of the anterior hypoconal wing in M^2.

It is worth noting that the additional material on upper dentition described in the present paper does not fully correspond to the morphology and measurements of the holotype of *Megaceroides algericus*. Unlike the holotype from Hammam Meskoutin, the additional material of *M. algericus* represents a deer form with somewhat smaller upper cheek teeth (length of M^1-M^3 tooth series amounts to 54.1 mm in the specimen from Guyotville against 58.5 mm in the holotype of *M. algericus*), the cingulum in upper molars of the additional material is not developed, while M^3 is significantly reduced in size (this specific size reduction in the specimen from Hammam Meskoutin is not observable). It is not clear yet if we observe here a broad individual variation in dental morphology or a true evolutionary process (see discussion below).

Lower mandible. The body of the lower mandible is very low and thick (Fig. 11). The symphyseal portion of the mandible is high (Fig. 12, Table 6). The diastemal part of the mandible is very short. The anterior portion of the mandible from M_1 to the symphysis has a cylindrical shape. Behind the M_1, the mandible becomes higher and more robust. The maximal thickness of mandible is behind M_3, in the area of the *Musculus masseter* insertion. The available fossil material does not display any clear sexual dimorphism of mandibular pachyostosis observed in *M. giganteus*. The juvenile mandible FIL 160 is already pachyostotic, although it is less thick than the mature specimens. The lower side of the horizontal part of the mandible is convex. The *processus angularis* is moderately expressed. The ascending part of the mandible is sloped backward and forms with the horizontal body of the mandible an angle amounting to 60º. The posterior side of the ascending ramus is concave. The coronoid processus is short and cone-shaped. The shape of the condylar articulation is cylinder-like. The distance between the cranio-mandibular condylar articulation and the M_3 is relatively large when compared to the majority of deer involved in the comparative study. This morphological trait is in accordance with the forward displacement of the upper tooth rows. The lower tooth row is displaced orally due to the very short diastema and obliquely set ascending portion of the mandible (Fig. 13).

Lower teeth. The crowns of lower cheek teeth are relatively small and rather short and broad (Table 7). At the initial stage of wear, protoconid and hypoconid of P_4 may not be completely fused (Fig. 11(B)); however, the fourth premolar usually shows a complete molarization with complete conjunction of protoconid and hypoconid at a more advanced

stage of wear. The size of the crown of P_2 is much reduced, so it remains untouched even in a deeply worn dentition, as may be seen in the specimen FIL166 (Fig. 12).

The specific proportions of lower tooth row are characterized by relatively reduced size of M_3, when compared to the larger and broader M_2 and M_1. The premolar series is comparatively short,; however, a broad variation is observed here. The premolar/molar length ratio amounts to 60.5% in the mandible FIL166, while the same tooth series ratio in the two specimens from Phacocheres amounts to 45.0% and 52.9% (Hadjouis, 1990).

Dental wear. The dental wear in *Megaceroides algericus* brings interesting details that reveal some earlier overlooked anatomical and paleoecological peculiarities of this species. The entire lower tooth row is evenly worn (with exception of P_2, which is not worn) in all studied specimens of *M. algericus*, unlike in the majority of deer, which normally show a more advanced wear of M_1. The statistical processing of mesowear traits is not possible because of the poorly preserved dental material; however, some observations are worth mentioning. The character of the tooth row wear varies, suggesting a rather broad range of food habits in *Megaceroides algericus*. Generally, the dental cusps are very low and rounded; nonetheless, the wear surface of the enamel in the majority of specimens available for observation is finely polished, suggesting a predominant dental attrition. However, the grinding surface of the mandible FIL166 is striated by transverse traces of wear caused by a coarse forage material. The direction of wear traces forms an angle of 60º with the tooth row axis. This observation suggests a comparatively wide angle formed by hemi-mandibles, which apparently attained 60º (Fig. 14). Such a broad angle between hemimandibles is in accordance with the particularly broad skull.

Antlers. The complete antlers of *Megaceroides algericus* are unknown. The cranium from Guyotville preserved only the proximal parts of the antlers. The left antler is broken just at few centimeters above the burr, while the right antler is broken 20 cm above the burr. The antlers are normally developed (the beam diameter is not disproportionally thin with respect to the burr size and to the diameter of pedicle) and do not show any sign of "degeneration" reported by Azzaroli (1979). The proximal portion of the right antler beam is straight and directed sideward, backward and slightly upward. The antler beam is cylinder-shaped and somewhat more robust than the supporting pedicle. The antero-posterior diameter of the right antler beam above the burr amounts to 53.0 mm, whereas the latero-medial diameter amounts to 56.0 mm. The same measurements of the left antler amount to 53.3 mm and 55.5 mm, respectively. The basal tine is not present in *Megaceroides algericus*. The next middle (or anterior) tine is inserted on the anterior side of the beam. The cross-section of the basal part of the middle tine is ellipse-shaped (its maximal diameter amounts to 40.6 mm, whereas its

minimal diameter amounts to 22.0 mm). The distance between antler burr and the base of the middle tine amounts to 96 mm. The antero-posterior diameter of the antler beam between the burr and the middle tine amounts to 42.4 mm. The height of the middle tine ramification is 140 mm. The antler becomes flattened in the area of the middle tine insertion and the above situated distal portion of antler extends into a palmation; the maximal diameter of antler above the middle tine (where the antler is broken) amounts to 59.3 mm, whereas the minimal diameter at the same level is 41.3 mm.

5. Discussion

5.1. Evolutionary significance of pachyostosis

The extreme cranial pachyostosis of *Megaceroides algericus* requires a special discussion here. There are few examples of pachyostosis among mammals. Most of the cases are known in ruminants, including cranial and mandibular pachyostosis in cervids (Morales et al., 1992). The pachyostosis of limb bones recorded in the lower Miocene giraffoid *Lorancameryx pachyostoticus* from Spain represents another phenomenon of bone thickening recorded in ruminants (Morales et al., 1992). Although the character of pachyostosis in *Lorancameryx* differs histologically and physiologically from the cranial bone thickening in cervids, Morales et al. (1992) regard both cases as different manifestations of the similar physiological and evolutionary process.

Morales et al. (1992) noticed that the limb bone pachyostosis in *Lorancameryx* occurred at the same geological epoch when several groups of ruminants evolved horns and horn-like cranial appendages. Therefore, according to these authors, the pachyostosis and the bony cranial appendages represent a similar physiological response to environmental changes and acted as "bone sinks" where excess tissue was stored during the growth seasons where nutrition vegetation was abundant. According to them, the pachyostosis of cervids could also represent a similar secondary metabolic response to exogenic factors, primarily marked seasonality.

The inert bone tissue was deposited in *Lorancameryx* on the limb bone diaphysis (especially on radius and ulna) every year starting from the subadult age (Morales et al., 1992), while in *Megaloceros giganteus* the mandibular pachyostosis developed through deposition of additional lamellar bone tissue during the early adult age; no visible changes in the state of pachyostosis were recorded during the subsequent adult life (Lister, 1994). According to Morales et al. (1992), the tissue of pachyostotic bone in *Megaceroides algericus* and *Sinomegaceros pachyosteus* shows the annual cyclic rhythm as in the case of *Lorancameryx*. Therefore, it seems that the pachyostosis of *Megaceroides algericus* has a

different physiological and ontogenetic background than the pachyostosis of *Megaloceros giganteus*.

Several authors repeatedly reported the development of mandibular pachyostosis in *Praemegaceros* and some other large-sized cervid forms (Kahlke, 1958, 1965; Azzaroli, 1979, 1994; Vislobokova, 1990, 2009, 2012a, 2012b, 2013). According to them, such development represent a specific side effect of gigantism in cervids and is regarded as an important taxonomical character distinguishing the phylogenetic branch of giant deer from other phylogenetic branches within the subfamily Cervinae. However, a simple scatterplot of mandible proportions shows that the mandible shape in large-sized *Praemegaceros* is very similar to the morphological condition found in *Eucladoceros* and *Dama* (Croitor, 2006). Van der Made and Tong (2008) found signs of mandibular pachyostosis in a wide variety of cervids and assumed that this specific character converged several times among cervids and denied its evolutionary significance for the phylogenetic group of giant deer. Therefore, the sporadic occurrence of mandibular pachyostosis in various cervid lineages cannot be used as a meaningful taxonomic character at the tribe level. The well-expressed cranial and mandibular pachyostosis is recorded only in very few cervid genera, such as *Sinomegaceros* from Eastern Asia, *Megaloceros* from Central and Western Eurasia, and *Megaceroides* from North Africa. Vislobokova (2009) reports also the mandibular thickening in the late Miocene medium-sized forms of the genus *Praesinomegaceros* from South Siberia.

Kahlke (1958) studied the variation of the cross-sections of mandibles in *Sinomegaceros pachyosteus* from Choukoutien and suggested that the mandible thickening in this deer is a dimorphic character. Kahlke (1958) also assumed that the increased mandible thickening in *S. pachyosteus* was a gradual evolutionary process. Nonetheless, the mandibular pachyostosis in *Sinomegaceros* evolved much earlier in another much smaller form with small antlers. Tleuberdina (1982) reported a rather small-sized late Neogene species (the estimated body mass based on dental measurements did not exceed 50 kg): *Sinomegaceros robustus* from South-East of Kazakhstan. The roe-deer sized *S. robustus* is characterized by primitive unmolarized P_4, small antlers with distal palmations (burr diameters amount to 18.0 and 16.2 mm), and pachyostotic lower mandible with almost circular cross-section (Tleuberdina, 1982). According to Shikama and Tsugawa (1962), some degree of pachyostosis is recorded also in *Sinomegaceros yabei*. Three mandible specimens of *S. yabei*, two of which certainly belong to a male, are characterized by a rather moderate degree of pachyostosis similar to the specimens of *M. giganteus* tentatively ascribed to females by Lister (1994) and Croitor et al. (2014).

Lister (1994) supposed that pachyostosis represents an adaptation that enhanced the skeletal calcium store, related to the large size of antlers. Croitor (2006) supported this point of view, noting that the enhanced mineral storage in head skeleton is an important physiological adaptation enabling the fast growing of large antlers during the relatively short vegetation season. Perhaps the pachyostosis in *Megaloceros giganteus* was physiologically connected with such specific giant deer morphological characters as an ossified vomer, complete and early obliteration of cranial sutures, diminished size of foramen ovale, and the development of additional enamel folds (i.e., cingula) at the base of molars in some evolutionary advanced populations of giant deer (Croitor, 2006). As far as concern cervids, Sanchez-Villagra (2010) reported an exceptionally high number of cranial suture fusions in *Megaloceros giganteus* (20 cranial sutures in the giant deer against 10 in the modern elk *Alces alces*); nonetheless, he excluded the simple mechanical adaptation of the advanced bone suture fusion to large and heavy antlers. The high number of suture fusion in giant deer contrasts with the general trend of ruminants toward the decrease in the number of fused cranial sutures, which is not correlated with body size and apparently represent a specific biomechanical adaptation to rumination (Bärmann and Sanchez-Villagra, 2011).

Therefore, one can assume that the high number of cranial suture fusion in *Megaloceros giganteus* represents another specific consequence of pachyostosis. However, Bärmann and Sanchez-Villagra (2011) report the high number of cranial suture fusion also for some other ruminant genera (*Ocapia*, *Tragelaphus*, *Kobus*, and *Antilocapra*), seeking the explanation in biomechanical factors. Van der Made and Tong (2008) remarked that the function of temporary storage of minerals should be followed by signs of resorption in pachyostotic mandibles. Actually, even non-pachyostotic bones represent a dynamic system constantly undergoing resorption and deposition of minerals and no particular "scars" of resorption on bone tissue could be seen, taking apart pathological cases (Alberts et al., 1983). Vislobokoba (2009, 2012b, 2013) regards the cranial pachyostosis of *Megaloceros giganteus* as a mechanical adaptation (comparable to cranial pneumatization in *Rangifer* and *Bison*) correlated with large and heavy antlers and reports a comparatively weak development of cranial pachyostosis in females of giant deer. This hypothesis is questionable for several reasons. The lower mandible is a suspended structure that is not actually exposed to the weight load of antlers and cannot have any function of weight support in the skull. It is not clear in this case which biomechanical advantage could bring a pachyostotic mandible, since the low-crowned and relatively small cheek teeth, the low *corpus mandibulae* and the relatively small area of insertion of *Musculus massetter* in *Megaloceros giganteus* and *Megaceroides algericus* suggest that their thick lower mandibles cannot represent any

particular mechanical reinforcement advantage (Croitor, 2006). Besides that, the pachyostosis is recorded also in the small-sized cervid with tiny antlers *Sinomegaceros robustus*.

It seems that pachyostosis and accessory cranial bone structures in ruminants such as horns and horn-like cranial appendages changed their functional significance during their large-scale evolutionary history (Janis, 1982). As cervid antlers, pachyostosis originally could serve as "bone sinks" where the excess bone tissue was stored (Morales et al., 1992). It is worth noting that all known pachyostotic cervids belong to the subfamily Cervinae and evolved and lived in the most peripheral and extreme parts of the distribution area of this subfamily. This is the case of the periglacial cursorial open landscape giant *Megaloceros giganteus*, the forest dwellers of the genus *Sinomegaceros* that may habe been affected by the repeatedly advancing arid zones of Central Asia, and *Megaceroides algericus* that evolved in very unusual environments for cervids (see discussion below), which strongly modified its skeletal morphology. Those species were exposed to the most stressing seasonal environmental conditions among Cervinae, supporting therefore the hypothesis of Morales et al. (1992). Another argument favouring the hypothesis of similar physiological-evolutionary origin of pachyostosis and antlers in cervids may be sought in the comparison of subfamilies Cervinae and Capreolinae. It seems that the pachyostosis is a peculiar physiological property of the subfamily Cervinae (not tribe Megacerini), which sporadically appears in some specific environmental conditions. Indeed, pachyostosis is not known among Capreolinae, however, some members of this subfamily are known to have antlers in females. The best known example is *Rangifer tarandus* inhabiting the most extreme environmental conditions among Capreolinae, but the occasional presence of small antlers in normally developed females also was reported for *Odocoileus* and *Capreolus* (Wislocki, 1954).

Therefore, the cranial pachyostosis in *Megaceroides algericus* initially represented a specific physiological mechanism characteristic of some lineages of Cervinae that evolved in extreme seasonal environments. Cervid pachyostosis is not correlated with body mass and size of antlers, since it is recorded in small-sized (*Sinomegaceros robustus*), medium-sized (*Megaceroides algericus*), and large-sized (*Megaloceros giganteus*) cervids. However, all known cases of pachyostosis are combined with palmated antlers (but the opposite affirmation is not true: many cervids with palmated antlers do not show any pachyostosis), suggesting that palmated antlers have not only social evolutionary significance, as it was suggested by Geist (1998), but also a specific environmental and physiological background.

5.2. *Paleoecology of* Megaceroides algericus

Regarding the pachyostosis of *Megaceroides algericus*, some of the peculiar traits distinguishing this species from the pachyostosis in *Megaloceros* are noteworthy. Not all parts of the skull in *Megaceroides* are equally pachyostotic: zygomatic arches and anterior part of mandible are comparatively weak and not reinforced by pachyostosis. Weak (or better to say, normal-sized) zygomatic arches are needed to ensure the movements of lower jaw, the likely reason why they are not affected by distorting pachyostosis. The bony rim of orbits and very broad forehead are particularly pachyostotic and ensure protective shelter for weak zygomatic arches. Other parts of the skull (rostrum, braincase) and the posterior part of mandible are also strongly pachyostotic and create a sort of bony helmet. At present, it is difficult to affirm if the cranial pachyostosis in *Megaceroides algericus* is a matter of sexual dimorphism. The only two known well-preserved skulls belong to males. The rather small series of available lower mandibles does not show any visible dimorphism. Ontogenetically, the pachyostosis of *Megaceroides algericus* is also specific. Taking into account the juvenile mandible FIL160 from Filfila and the pachyostotic mandible with deciduous teeth from the grotto of Chenoua (Algeria) figured by Arambourg (1938: fig. 8A), the additional bone tissue deposition started in *Megaceroides algericus* from an early juvenile age, unlike in *Megaloceros giganteus*. As it was already mentioned above, the tissue of pachyostotic bone in *Megaceroides algericus* shows an annual cyclic rhythm and therefore increases with age at least during some periods of the individual's life (Morales et al., 1992).

Whatever the initial significance of the cranial pachyostosis, it seems that it acquired a new function in *Megaceroides algericus*. Apparently, the unusual cranial specialization of *M. algericus* is a result of adaptation to an ecological niche, which was unavailable for ecologically highly competitive (*fide* Geist, 1998) African bovids. There are no morphological analogies among modern species of deer or other ruminants that could help in the paleoecological interpretation of *M. algericus*. The anterior part of the mandible, the zygomatic arches and the dentition remain comparatively weak, contrasting with the pachyostotic bones of cranium and the posterior part of the mandible. The *processus coronoideus* of the lower jaw is short and cone-shaped, and the area of insertion of the *musculus masseter* is rather small. Taking into account the studies of cranio-dental adaptations in ruminants (Caloi and Palombo, 1995; Janis, 1995; Palombo, 2005), the enlisted characters suggest that *M. algericus* had quite low mastication abilities and was not adapted to process a hard fibrous forage material. The rather weak mastication ability is suggested also by the oral (i.e., anteriorly directed) shift of cheek tooth row resulting in a decrease of power moment. The flat and broad skull with broad muzzle of *M. algericus* is vaguely reminiscent of specific cranial shape of semiaquatic herbivorous mammals such as hippopotamuses. The

weak mastication abilities and small low-crowned cheek teeth suggest a semiaquatic or periaquatic habitus for *M. algericus* with a foraging specialization on soft water herbage. The reduced preorbital fossae could be another adaptation to a periaquatic habitat, since the peorbital fossae are very small in the modern Chinese water deer *Hydropotes inermis* (Flerov, 1952). Another specific morphological character of *Megaceroides algericus* may be found in the images of this animal from the Paleolithic art. Camps (1992) published several Paleolithic images of this deer that show an unusual, very long tail for a cervid. Among modern cervids of similar body size, the relatively long tail is characteristic of *Elaphurus davidianus* specialized to humid swamp habitats (Flerov, 1952).

The assumption of semiaquatic or periaquatic habits of *M. algericus* is further supported in the majority of the studied specimens by the finely polished grinding surfaces of cheek teeth resulting from attrition (Fortelius and Solounias, 2000). However, the low dental cusps and the grinding surface of lower mandible FIL166 striated by transversal traces of wearing caused by a coarse forage material, suggest that the animals were regularly exposed to a stressing shortage of forage, apparently during the dry seasons, as it was already shown, e.g., for the modern plains zebra *Equus burchelli* (Kaiser and Schulz, 2006). The regular exposure to unfavorable seasonal conditions is also supported by the cyclic rhythm of pachyostosis development noticed by Morales et al. (1992).

Cranial helmet-like pachyostosis in *M. algericus* could have had a function of passive defense against water predators such as crocodiles, which represent the most frequent danger in African periaquatic biotopes (Croitor, 2014). Crocodiles were present in the area of distribution of *Megaceroides algericus* in the past and survived in the region until the middle of the XXth century (Brito et al., 2011). The head of foraging deer is the important part of body most exposed to predator's attacks. The early ontogenetic development of pachyostosis in *M. algericus* supports this hypothesis, since this character must be vitally important for juveniles too. The thick cranial and mandibular bones must protect animal's head from deep lethal wounding and therefore increase chances of animal to escape from a predator. The cranial pachyostosis inherited from forerunners by *Megaceroides* should be regarded here as a good example of preadaptation that was maintained by natural selection in new conditions such as the adaptation of passive defense. The robust radius and ulna described by Pomel (1893) could be part of such adaptation, permitting to resist the attempts of a crocodile to drag its prey underwater.

Taking into account the brachyodont dentition and shallow mandibular body combined with sideward-oriented antlers and large tympanic bullae, Abbazzi (2004) arrived to the rather opposite conclusion that the small-sized *M. algericus* was an open-landscape browser (Janis,

1995). Although Abbazzi (2004) reports the large size for upper and lower teeth, this is not the case: the cheek teeth of *M. algericus* are relatively small, marked by particular size reduction of premolars as well as M^3 and M_3. Nonetheless, the brachyodont M^{1-2} and M_{1-2} are relatively broad, representing in my opinion a sort of grinding millstones for soft water plants.

The fauna associated with *M. algericus* is quite ecologically heterogenous and may be regarded as a mammal assemblage that inhabited an ecotone close to water bodies. The faunas from Ain Tit Mellil (Morocco) and Filfila (Alger) contain semiaquatic species such as *Hippopotamus amphibius*, forest dwellers as *Sus scrofa algeriensis*, woodland species as *Bos primigenius* and *Taurotragus*, and open landscape species as *Connochoetes taurinus*, *Crocuta spelaea*, and *Camelus sp*. (Arambourg, 1939; Hadjiouis, 1990).

5.3. Systematic position of the genus Megaceroides

Determining the systematic position of such an odd and very specialized species as *Megaceroides algericus* within Cervinae is not an easy task. However, even if the cranial morphology of *M. algericus* shows some highly specialized traits, the correct assessment of plesiomorphic and apomorphic characteristics allows for revealing the phylogenetic relationships, and thus systematic position of this North African endemic lineage.

Megaceroides algericus shows most significant morphological differences with the genus *Cervus* and allied forms. Unlike deer of the *Cervus* group (genera *Cervus*, *Hyelaphus*, *Rusa*, and *Pannolia*), *M. algericus* is characterized by a broad bell-shaped basioccipital (as modern *Axis*, *Rucervus*, *Dama*, and the majority of extinct genera of Western Eurasia), relatively large and rounded *bulla tympani* (as *Dama*), missing upper canines (as *Dama* and *Megaloceros*), and long nasal bones that extend behind the anterior edges of orbits. Excluding pachyostosis as a peculiar specialization, one can notice that *Megaceroides* possess an advanced cranial morphology when compared to *Cervus* and allied from Southern and Eastern Asia. These cranio-dental morphological differences suggest that the *Megaceroides* and *Cervus* lineages diverged as early as the late Miocene.

Obviously, *Megaceroides* does not belong to the phylogenetic branch of the genus *Praemegaceros* as it was suggested by Azzaroli (1979) and Vislobokova (2013). Unlike *Praemegaceros*, *Megaceroides* is characterized by the relatively longer braincase (a primitive character), the cylinder-shaped pedicles (not compressed antero-posteriorly or dorso-ventrally if considering their strong posteriorward and sideward inclination on the skull, as in some advanced species of *Praemegaceros*), the cranial and mandibular pachyostosis, and the long nasal bones (Croitor, 2006). The long nasal bones of *Megaceroides* extended behind the imaginary line connecting anterior edges of orbits represent a good taxonomic character, but

are of little interest for the systematic and phylogenetic study, since they probably represent here an apomorphic character. However, the relatively long braincase of *Megaceroides* is an important primitive character that rules out a direct phyletic relationship with geologically older, but in this case more advanced *Praemegaceros*. The cylindrical shape of pedicles in *Megaceroides* also suggests that this genus is not related to the advanced middle Pleistocene species of *Praemegaceros* (*P. verticornis* and *P. solilhacus*), which evolved the biomechanically more advantageous dorso-ventrally compressed and latero-medially extended pedicles that acted as a reinforced support with increased area of cross-section for large and heavy antlers (Croitor, 2006). The peculiar dorso-ventrally compressed shape of pedicles is maintained even in the secondary dwarfed *P. dawkinsi* with diminished antlers.

The cranial and dental morphology of *Megaceroides* and *Dama* shows some similarities (Table 8). *Megaceroides* shares with *Dama* the broad bell-shaped basioccipital, the large orbits, the large rounded bulla tympani, the flexed braincase, the long nasal bones (however, this character is also apomorphic in *Dama*; Croitor, 2014), the missing upper canines, and the similar proportions of lower tooth row: PP/MM in *Megaceroides* varies between 45.0% and 60.5%, while in modern *Dama dama* this ratio varies between 46.0% and 61.6% (Croitor, 2014). Unlike *Dama*, the braincase of *Megaceroides* is somewhat less flexed; the parietal and frontal bones are flat; the pachyostosis is strongly pronounced (it is completely absent in *Dama*); the rather long pedicles are set obliquely on the skull (not short and vertically oriented as in *Dama*); the ethmoidal vacuities are completely closed, and upper molars are supplemented with a variable lingual cingulum. Such cranial characters as the less flexed braincase and obliquely set frontal pedicles define *M. algericus* as a more primitive cervid form than the fallow deer. The closed ethmoidal vacuities in *M. algericus* apparently resulted from the pachyostosis of face bones.

Megaceroides and *Megaloceros* share the developed cranial pachyostosis, the bell-shaped basioccipital, the missing upper canines, the presence of a variable cingulum in upper molars, and long nasal bones extended behind the imaginary line connecting the anterior edges of orbits (Table 8). The shape and relative length of the braincase, the position of the antler pedicles, the developed cingula in upper molars, and the cranial hyperostosis of *Megaceroides algericus* suggest its greater affinity with *Megaloceros giganteus*. Unlike *Megaloceros*, *Megaceroides* is characterized by enlarged rounded bulla tympani, a flexed braincase, a lacking basal tine, and relatively larger orbits with respect to the condylo-basal length. However, the relatively large orbits may be a secondary effect caused by the shortened splanchnocranium. It seems that proportions of the lower tooth series in *Megaceroides* (PP/MM = 45.0%, 52.9%, 60.5%; Croitor, 2014) tend to be more advanced than in

Megaloceros giganteus from Ireland (PP/MM = 53.6-61.1%, based on the sample stored in NHML), and significantly more advanced (according to evolutionary trends in Cervidae described by Vislobokova, 1990) than in the primitive form of *Megaloceros giganteus* from Bisnik, Poland (PP/MM = 61.9-65.6%; Croitor et al., 2014). The analysis of cranial characters of various Eurasian cervids presented here supports the old assumption of Joleaud (1914) on intermediary morphological and systematic position of *Megaceroides* between *Megaloceros* and *Dama*. In addition, the peculiar combination of cranial and dental characteristics of the African deer confirms the reasonability of the erection of *Megaceroides* at the generic level proposed by Arambourg (1932, 1938).

Molecular phylogenetic studies has revealed that the fallow deer is the closest extant cervid species to *Megaloceros giganteus*, although the evolutionary divergence between *Megaloceros* and *Dama* has occurred very early, 4-5 Myr (Lister et al., 2005) or even 10.7 Myr (Hughes et al., 2006). The close phylogenetical relationship between *M. giganteus* and *D. dama* is also supported by some shared characteristics of the cranial morphology: both species show a relatively long braincase, long nasal bones (synapomorphy), a relatively short orbito-frontal portion of the skull (the anterior edge of the orbit is situated above M^2), missing upper canines, and a similar shape of the broadened basioccipital at the level of the pharyngial tuberosities. Pfeiffer's (1999) suggestion on close relationship between the giant deer and the red deer based on a postcranial morphology analysis is disputable. The use of postcranial morphological characters in phylogenetic reconstructions is unsafe since limb bones are greatly influenced by various environmental and biomechanical factors such as landscape features, ground surface properties, type of locomotion, body mass, social behavior, etc. (Köhler, 1993). The lack of studies analyzing the plesiomorphic or apomorphic nature of postcranial characters represents the main methodological issue here. Indeed, a phonetic (cluster) analysis of postcranial characters reveals ecological and biomechanical similarities rather than a genuine phylogenetic signal. The molecular phylogeny research carried out by Kuehn et al. (2005) suggests a close relationship between giant deer and red deer, but, according to Hughes et al. (2006), these results come from a wrong determination of fossil specimens or from contamination during the DNA amplification process. The genetic evidences of a close relationship between the giant deer and red deer obtained by Kuehn et al. (2005) is "almost certainly the result of contamination" (A. Lister, pers. comm.).

With the lacking basal tine (Fig. 15), the palmated antlers of *Megaceroides algericus* are of minor significance for the present study, since palmations may have evolved independently in different phyletic lineages, while the basal tines have tend to reduce in cervid forms with secondary reduced body size, as for instance in *Praemegaceros dawkinsi*

and numerous dwarfed insular species (Azzaroli, 1961; Azzaroli, 1979; Caloi and Malatesta, 1974; Croitor, 2006; Croitor et al., 2006).

Azzaroli (1953), Thomas (1979) and Hadjiouis (1990) noticed that the shape of the lower mandible and skull of *Megaceroides algericus* is similar to the mandible of *Simomegaceros pachyosteus* from Choukoutien (China). At least superficially, the skull shape of *S. pachyosteus* with its little flexed braincase, broad orbito-frontal part, and short splanchnocranium seems to be a less accentuated version of *M. algericus*. *Megaceroides* is characterized by the presence of a well-developed middle tine, which normally is lacking in *Sinomegaceros* (Shikama and Okafuji, 1958; Shikama and Tsugawa, 1962; van der Made and Tong 2008). Van der Made and Tong (2008) regard the absence of the middle tine as an essential diagnostic character of *Sinomegaceros* that is shared with *Arvernoceros*. However, a small knob-like vestige of the middle tine is present in some specimens of *S. pachyosteus* (Kahlke, 1958), calling for some caution here. The distribution area of the genus *Sinomegaceros* in Eastern Asia was latitudinally limited between 25° and 50°. According to Vislobokova (2012a, 2012b, 2013), *Sinomegaceros* was the southern ecological counterpart of *Alces* and, therefore, could not disperse northward and westward because of the ecological competition with *Alces*. Van der Made and Tong (2008), taking into account the combination of dental, antler, cranial, and postcranial characters in large-sized deer from Western and Eastern Eurasia, exclude the possibility of westward migrations of large-sized deer from the eastern part of Asia. Considering this, the cranial shape affinities between *Sinomegaceros* and *Megaceroides* could result from convergence. Ultimately, only an extensive morpho-functional study of the cranial and skeletal morphology of *Sinomegaceros* may clarify the nature of this convergence.

5.4. Taxonomical context of Megaceroides algericus

The taxonomical significance of the rather variable dental characters of *Megaceroides algericus*, such as the varying cingulum in upper molars and the broad variation of tooth row proportions, is still unclear. Possibly, we are dealing in this case with chronological forms of the endemic North African deer: an older larger form from Hammam Meskoutin with strong cingulum and normally developed M^3, and a more specialized descendant form with smaller dentition, reduced cingulum and marked reduction of M_3 and M^3. One can assume that the thick-jawed deer described by Pomel (1892) and figured in Pomel (1893) represents a late form defined by relatively smaller M_3 (Table 7). In that case, Pomel's (1892, 1893) name *Cervus pachygenys* proposed for the African Neolithic cervid form with pachyostotic mandibles and upper molars without cingulum could be used at least as the subspecies tank –

Megaceroides algericus pachygenys (Pomel, 1892) – and the lower mandible from Berrouaghia (Algeria) described and figured by Pomel (1892, 1893: pl. VII-VIII) should be regarded as the holotype of *M. algericus pachygenys*.

The taxonomical position of the genus *Megaceroides* needs also to be clarified. Viret (1961) proposed to place the giant deer in a separate tribe Megacerini based on the genus *Megaceros* Owen, 1844. This point of view is accepted and defended by Vislobokova (1990, 2009, 2012a, 2012b, 2013) and di Stefano and Petronio (2000-2002). According to Lister (1987), the genus name *Megaloceros* Brookes, 1828 has priority over *Megaceros* Owen, 1844 and this viewpoint was accepted uncritically. Later on, Lister (1994) substituted Megacerini Viret with Megalocerini and supposed that *Dama* could be the only extant genus of this tribe. Abbazzi and Masini (1997) quoted Lister's tribe name as Megalocerini Viret, 1961. Vislobokova (2009) accepts the genus name *Megaloceros*, however she continues to use the tribe name Megacerini based on *Megaceros*. Grubb (2000) pointed out that Megacerini Viret, 1961 is a junior synonym of Megalocerotinae Brookes, 1828. Therefore, the correct name of the tribe should be Megalocerotini Brookes, 1828. According to Grubb (2000), the genera *Praemegaceros*, *Megaceroides*, *Megaloceros*, and *Sinomegaceros* belong to the tribe Cervini Goldfuss, 1820, therefore Megalocerotini Brookes, 1828 is a synonym of Cervini Goldfuss, 1820.

Vislobokova (1990, 2009, 2012a, 2012b; 2013) considers that the tribe of giant deer includes eight genera: *Megaloceros*, *Praemegaceros*, *Sinomegaceros*, *Praesinomegaceros*, *Praedama*, *Orchonoceros*, *Arvernoceros*, and *Neomegaloceros*. In my opinion (Croitor, 2006), the quoted list of genera represents a rather eclectic group including forms that belong to several different phylogenetical stocks, as well as poorly known cervid forms, such as *Neomegaloceros gracilis* and *Praedama savini* (see discussion below).

Radulesco and Samson (1967) and Azzaroli and Mazza, (1992, 1993) regard *Eucladoceros* as a primitive forerunner of *Praemegaceros*, seeking support for this hypothesis in the homologous general construction of antlers. Moreover, *Praemegaceros* shares essential cranial characteristics and antler morphology with *Eucladoceros*. The direct phylogenetical relationship between those two genera has been accepted by many authors (Radulesco and Samson, 1967; Azzaroli, 1979; Azzaroli and Mazza, 1993; Abbazzi, 2004; Croitor, 2006, 2014). Earlier, I proposed to include *Praemegaceros* and *Eucladoceros* together with *Orchonoceros* in the tribe Eucladocerini (Croitor, 1997), but, according to the current state of knowledge, this tribe name also falls under synonymy with Cervini Goldfuss, 1820.

The assumed direct phylogenetical relationship between *Megaloceros* and *Praedama* is based on a single character, the flattened basal tine (Azzaroli, 1953; Vislobokova, 1990;

Van der Made and Tong, 2008). The fine series of antler material from Forest Bed (stored in NHML) and the complete antler from Suessenborn, Germany (Kahlke, 1969: table XXXIV) show a series of characters that suggests a significant morphological distance between *Praedama savini* and *Megaloceros giganteus*: unlike the giant deer, the antler base in *Praedama savini* is characterized by a specific quadrangular cross-section, while the whole antler (compressed from the sides) and the dichotomous pattern of bifurcation of crown tines rather reminds *Eucladoceros* (Croitor, 2014). The flattened proximal part of basal tine of *Praedama savini* (the complete basal tines are unknown) that is regarded as a good argument for close relationship between *Megaloceros* and *Praedama*, is also characteristic of *Eucladoceros dicranios*. The dental and mandibular remains of *Praedama* from Cueva Victoria do not show any trace of cingulum in upper molars and have no clearly expressed mandibular pachyostosis (van der Made, 2014). The skull morphology of *Praedama* is unknown; therefore, well-founded arguments on phylogenetic relationships of this endemic European genus for the present moment are missing. We need more fossils and better arguments that will help to reveal the systematic position and phylogenetic relationships of *Praedama*.

Arvernoceros ardei is another species, which was regarded as a forerunner of *M. giganteus* because of its palmated basal tine and isolated upper molars with cingulum (Heintz, 1970). The very large-sized deer *Arvernoceros verestchagini* from the early Pleistocene of Eastern Europe and Greece maintained a rather simple antler construction, a simple unmolarized lower fourth premolar, and lacks a cingulum, hyperostosis, and other characters that undoubtedly could indicate a relationship with *Megaloceros* (Croitor and Kostopoulos, 2004). The general pattern of antler construction of *Arvernoceros* recalls that of *Sinomegaceros* (van der Made and Tong, 2008) and modern *Rucervus* (Croitor, 2009). According to genetic data, *Rucervus duvaucelii* has a rather isolated position among modern Cervinae, having diverged very early (late Miocene) from the main group of Old World deer together with *Axis axis* (Pitra et al., 2004).

The last problematic deer, *Neomegaloceros gracilis* from the late Miocene of Ukraine was proposed by Korotkevich (1971) as a forerunner of *Praemegaceros verticornis* since its antler is characterized by a distal palmation and an additional tine, which was interpreted as homologous to the posterior tine in *Praemegaceros*. The first tine of *Neomegaloceros* is situated very high on the anterior side of the beam. The antler beam in *Neomegaloceros* is not curved in the areas of first and posterior tines as in *Praemegaceros*. The general antler shape of *Neomegaloceros* does not show any similarity with antlers of *Praemegaceros*. The distal palmation of the antler is regarded by Korotkevich (1971) as an important character proving

the direct phyletic relationship between *Neomegaloceros* and *Praemegaceros*. However, the palmated antlers appear only in the most advanced forms of *Praemegaceros*, while the earlier forms *Praemegaceros obscurus*, *P. pliotarandoides*, and *P. verticornis dendroceros* bear antlers without palmation (Azzaroli and Mazza, 1992, 1993; Croitor, 2006). The so-called "posterior tine" appears in several cervid lineages, represented by such genera as *Rangifer*, *Megaloceros*, *Praedama*, and some *Sinomegaceros*. It seems that this "posterior tine" developed several times independently in cervids adapted to open environments and, possibly, had a function of removing the flying parasites from the back in the rutting males, thus increasing their combat capacities. *Neomegaloceros* is a junior synonym of *Cervavitus* and belongs to the subfamily Capreolinae Brookes, 1828 (Croitor, 2006, 2014).

Therefore, the tribe of so-called giant deer *sensu lato* proposed by Vislobokova (1990, 2009, 2013) is a polyphyletic group that includes various lineages not only from the subfamily Cervini, but also from the subfamily Capreolini. Most of the cervids included by Vislobokova (1990, 2009, 2012a, 2012b; 2013) in the tribe of giant deer represent the peculiar eco-evolutionary type or "constellation" (*sensu* Geist, 1998) of open landscape giants with very large antlers (*Megaloceros*, *Praemegaceros*) and forest/woodland giants with smaller antlers (*Arvernoceros*, *Sinomegaceros*) approaching to the eco-evolutionary type of modern *Alces alces*.

The tribe Megalocerotini Brookes, 1828 *sensu stricto* should be restricted only to the genera *Megaloceros*, *Megaceroides*, and *Dama*, however, it is difficult in this case to propose a reliable differential diagnosis for this tribe. Grubb (2000) grouped all Old World deer with small or missing upper canines and large complicated antlers into the single tribe Cervini Goldfuss, 1820. Possibly, the tribe Cervini Goldfuss, 1820 could be restricted to the phylogenetic branch of *Cervus* and related genera (or subgenera) *Hyelaphus*, *Rusa*, *Panolia*, and *Przewalskium*, since this cervid group shares similar cranial and dental characteristics (e.g., the presence of small upper canines, the narrow triangular basioccipital) and genetic analysis revealed their monophyly (Pitra et al., 2004). However, the craniodental morphology of Plio-Pleistocene Eurasian Cervinae is still imperfectly known and data for the classification of the subfamily Cervinae at the tribal level are insufficient.

5.5. Zoogeographic context and origin

Limited by the Atlas Mountains from the South, the area of distribution of *Megaceroides algericus* has a refugial character, as also reported for many other African species of Mediterranean affinity (Brito et al., 2011). Joleaud (1916) assumed that *Megaceroides algericus* dispersed into Northern Africa through the Strait of Gibraltar.

According to Thomas (1979), the most plausible migration path for African deer is the "Libyan-Egyptian" way, i.e., via the south and south-east coast of the Mediterranean sea. Fernandez et al. (2015) consider that the way of dispersal across the Strait of Gibraltar seems to be more probable than the hypothetical arrival from the Libyan-Egyptian or Sicilian-Tunisian routes, which requires more evidences. So far, the remains of *Megaloceros*, the most probable forerunner of *Megaceroides algericus*, are unknown in southern Italy (Lister, 1994). On the other hand, undeniable remains of *Megaloceros giganteus* are reported only from the northern part of the Iberian Peninsula (Lister, 1994). The presence of giant deer in the area of Madrid (Sesé and Soto, 2000, 2002: p. 332, fig. 16) and in the fauna of Bolomor Cave near Valencia (Peris et al., 1997: p. 26) are based on poorly diagnostic material that needs a confirmation. Van der Made (2014) described *Megaloceros novocarthaginiesis* from the end of the early Pleistocene of Cueva Victoria, Spain. The new species is very close to *Praedama savini* (Dawkins, 1887) and differs from the latter only by a somewhat larger size and higher position of the basal tine. Therefore I prefer to include this species, pending confirmation of its taxonomic status, in the genus *Praedama*. Among noteworthy characters, the absence of any trace of cingulum in upper molars should be mentioned (van der Made, 2014).

The closer phylogenetic relationships between *Megaloceros*, *Megaceroides*, and *Dama* are supported also by paleobiogeographic data. The Mediterranean basin is the area of evolutionary radiation of the genus *Dama* (up to 7 fossil and modern species, including present day *Dama dama* from Anatolia and *Dama mesopotamica* from Near East), which is known only from Western Eurasia (Croitor, 2014). Until now, the highest taxonomic diversity of the genus *Megaloceros* is described from Western Europe (Azzaroli, 1953; Vislobokova, 2012a, 2012b, 2013). Therefore, *Megaceroides algericus* from the zoogeographic point of view is a part of evolutionary radiation of the *Megaloceros-Dama* lineage that took place in Western Eurasia and the Mediterranean area. The medium-sized cervid from the middle Pleistocene of Near East described by di Stefano (1996) as *Dama clactoniana mugarensis* is of special interest for the present discussion. This cervid form is characterized by a flattened antler beam, a flattened basal tine terminated by a bifurcation, and a well-developed cingulum in upper molars (di Stefano, 1996). The lower premolar series seems to be relatively long (66%, measured from the photographs in di Stefano, 1996) and represents a primitive condition similar to *Megaloceros giganteus* from Bisnik (Poland). The relatively robust radius of di Stefano's deer (radius length is *ca*. 215-220 mm and mid-shaft breadth is *ca*. 29 mm: di Stefano, 1996: fig. 8) is another character that distinguishes this cervid from the equal-sized representatives of the genus *Dama* and reminds the morphological condition described by Pomel (1893) in *Megaceroides*. Taking into account specific characters such as cingulum in

upper molars, low positioned flattened and bifurcated first antler tine, and flattened antler beam, one can assume that the medium-sized cervid from the Near East is a primitive or dwarfed form of the giant deer *Megaloceros mugarensis* (di Stefano, 1996) and may represent a transitional form between *Megaloceros* and *Megaceroides*. The medium-sized *Megaloceros mugarensis* (di Stefano, 1996) from the middle Pleistocene of Near East therefore appears as the most probable forerunner of *Megaceroides algericus*. An indirect support for this assumption is provided by Thomas (1979), who reports the earliest, while scanty and poorly preserved, cervid fossil remains from the middle Pleistocene of North Africa.

6. Conclusions

Megaceroides algericus from the late Pleistocene-early Holocene of Northern Africa is a highly specialized cervid that evolved in extreme geographical area and environmental conditions for the family Cervidae. The genus *Megaloceros* from the middle to late Pleistocene of the boreal latitudes of Eurasia is the closest phylogenetic relative to *Megaceroides*. The medium-sized *Megaloceros mugarensis* (di Stefano, 1996) from the middle Pleistocene of the Near East is the most probable forerunner of *M. algericus* and the linking form between *Megaloceros giganteus* and *Megaceroides algericus*. The most probable way of dispersal of *Megaceroides algericus* to Africa is the south-east coast of the Mediterranean sea, the so-called "Libyan-Egyptian" way.

The unusual cranial morphology of *Megaceroides algericus* is regarded here as a combination of ancestral morphological and physiological characteristics (first of all, cranial pachyostosis) and apomorphic characters (relatively diminished dentition with reduced size of P_2, P^2, M_3, and M^3, weak zygomatic arches and anterior part of mandible, short and broad splanchnocranium with orally shifted cheek tooth rows) that represent an ecological adaptation which permitted to avoid a direct competition with ecologically highly competitive bovids: the niche of a periaquatic or semiaqualic herbivore that feed on soft water plants. This hypothesis is supported by the generally weak dentition and other cranial structures that are involved in the forage processing. The unusually thick helmet-like cranial bones acquired the new function of passive defense against the predators that usually wait for their prey at watering places. Unlike *Megaloceros*, the pachyostosis in *Megaceroides* ontogenetically appeared earlier in juvenile individuals with deciduous cheek teeth and had several cycles of seasonal growth. Phylogenetically, *Megaceroides* belongs to the *Megaloceros-Dama* branch and stands close to *Megaloceros*.

The taxonomy of the subfamily Cervinae remains poorly understood at the tribe level. The tribe Megalocerotini Brookes, 1828 *sensu lato* (= Megacerini Viret, 1961 *fide*

Vislobokova, 1990, 2009, 2012a, b; 2013) appears as a polyphyletic group that includes large-sized specific eco-evolutionary types of cervids, which evolved independently in several lineages, and some poorly known forms that have similar apomorphic antler characters. The tribe Megalocerotini Brookes, 1828 *sensu stricto*, including only the genera *Megaloceros*, *Megaceroides*, and *Dama*, is likely to represent a genuine phylogenetic branch. However, it is difficult to give an adequate taxonomical definition for this restricted taxon containing highly specialized forms representing various eco-evolutionary types, first of all because similar cervid eco-evolutionary types can be found in other phylogenetic branches of the subfamily Cervinae Goldfuss, 1820 (Geist, 1998).

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Table and Figure captions

Table 1. Fossil material of *Megaceroides algericus* (Lydekker, 1890) from the National Museum of Natural History in Paris studied in the present work.

Table 2. Cranial measurements of the modern and fossil deer involved in the present comparative study. CBL, condylo-basal length; P^2-M^3, length of upper cheek tooth row; M^3-oc., distance between M^3 and posterior edge of occipital condyle; M^1-M^3, length of upper molar series; P_2-P_4, length of upper premolar series; P^2-pr., distance between P^2 and prosthion; or-pr., distance between orbit and prosthion; Dor., horizontal diameter of orbit; or-oc., distance between orbit and posterior edge of occipital condyle.

Table 3. Mandibular measurements of the modern and fossil deer involved in the present comparative study. C-P_2, length of diastema (distance between C and P_2); P_2-P_4, length of lower premolar series; M_1-M_3, length of lower molar series; M_3-art., distance between M_3 and mandibular articulation; gn.-M_1, distance between gnation and M_1; M_1-art., distance between M_1 and mandibular articulation; art.-gn., distance between mandibular articulation and gnation.

Table 4. *Megaceroides algericus* (Lydekker, 1890): cranial measurements.

Table 5. *Megaceroides algericus* (Lydekker, 1890): measurements of upper cheek teeth.

Table 6. *Megaceroides algericus* (Lydekker, 1890): measurements of lower mandibles. GM/1, unnumbered specimen from Grotte de la Madeleine with P_4-M_3; GM/2, unnumbered specimen from Grotte de la Madeleine with malformation.

Table 7. *Megaceroides algericus* (Lydekker, 1890): measurements of lower cheek teeth.

Table 8. Comparison of cranial characters and proportions (with respect to condylo-basal length, CBL) of *Megaceroides algericus*, *Megaloceros giganteus* and *Dama dama*.

Figure 1. Fossiliferous sites considered in the present study: **1**, Ain Tit Mellil (Morocco); **2**, Berrouaghia (Algeria), the type locality of *Cervus pachygenys* Pomel, 1892; **3**, Guyotville

(Algeria); **4**, Phacocheres (Algeria); **5**, Grotte de la Madeleine (Algeria); **6**, Filfila (Algeria); **7**, Hammam Meskoutin (Algeria), the type locality of *Cervus algericus* Lydekker, 1890.

Figure 2. *Megaceroides algericus* (Lydekker, 1890): male skull from Guyotville (now Ain-Benian, Algeria) stored in Paris (NMNH, "Collection Arambourg", no number). **A**. Side view. **B**. Frontal view. **C**. Palatal view. Scale bars: 5 cm.

Figure 3. *Megaceroides algericus* (Lydekker, 1890): semi-schematic drawing of the palatal view of the male skull from Guyotville showing the damaged parts (shaded). Scale bar: 5 cm.

Figure 4. The ratio between the length of face (measured from the anterior edge of orbit to prosthion) to the condylo-basal length of the skull of *Megaceroides algericus* from Guyotville compared to *Praemegaceros cazioti* (adapted from Caloi and Malatesta, 1974), *Praemegaceros obscurus* (IGF4024, adapted from Croitor, 2014), *Dama dama* (47.1.1.4, NHML), *Megaloceros giganteus* (M28968, NHML), and *Cervus elaphus* (Nr. 1927-58, NMNH).

Figure 5. The position of the upper tooth row in *Megaceroides algericus* from Guyotville compared to an insular dwarfed deer (*Praemegaceros cazioti*), large-sized deers (*Praemegaceros obscurus* and *Megaloceros giganteus*), and medium-sized continental deers (*Dama dama* and *Cervus elaphus*). The provenance of specimens involved in the comparison is indicated in the caption of Fig. 4.

Figure 6. Angle between the facial and neural parts of the skull. **A**. *Megaceroides algericus* from Guyotville. **B**. *Megaloceros giganteus ruffi* from Bruhl, Germany (Stuttgart Museum, adapted from Vislobokova, 2012b). **C**. *Dama dama* (ZMS, coll. 451, c.12058). Scale bars: 5 cm.

Figure 7. *Megaceroides algericus* (Lydekker, 1890): braincase MOC148 (NMNH) from Ain Tit Mellil (Morocco). **A**. Side view. **B**. Basal view. Scale bar: 5 cm.

Figure 8. *Megaceroides algericus* (Lydekker, 1890): semi-schematic drawing of the specimen MOC148 (NMNH) from Ain Tit Mellil (Morocco) showing damaged (shaded) and missing (dashed line) parts from the side view. Scale bar: 5 cm.

Figure 9. *Megaceroides algericus* (Lydekker, 1890): frontal view of the skull fragment MOC148 (NMNH) from Ain Tit Mellil (Morocco); *nas.*, posterior parts of nasal bones. Scale bar: 5 cm.

Figure 10. *Megaceroides algericus* (Lydekker, 1890): fragment of right upper jaw FIL169 (NMNH) with M^2 and M^3 from Filfila (Algeria). Scale bar: 3 cm.

Figure 11. *Megaceroides algericus* (Lydekker, 1890): lower mandible (dex., no number, NMNH) from Grotte de la Madeleine (Algeria). **A**. Lateral view of the mandible with transversal cross-sections taken in front of P_4 and behind M_3. **B**. P_4 in occlusal view. Scale bar: 5 cm.

Figure 12. *Megaceroides algericus* (Lydekker, 1890): lower mandible (sin., FIL166, NMNH) from Filfila (Algeria). Lateral view and dental grinding surface. Scale bar: 5 cm.
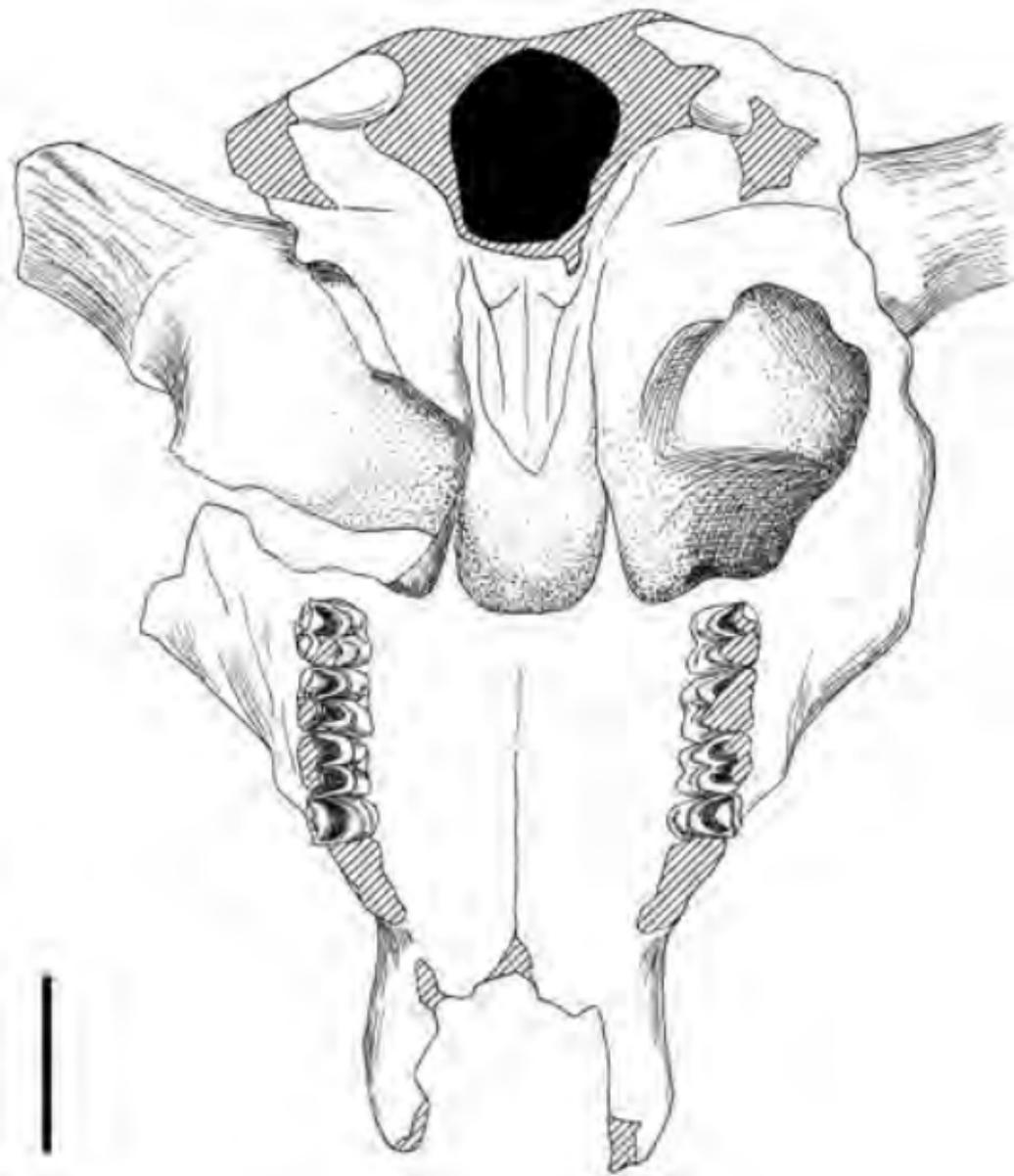
Figure 13. Proportions of lower mandible (FIL166, MNMH) of *Megaceroides algericus* compared to *Muntiacus muntjak* (ZMS, c.780), *Hydropotes inermis* (ZMS, c.1441), *Dama dama* (ZMS, c.12061), and *Praemegaceros cazioti* (COS19040, adapted from Croitor et al., 2006). M3-art., distance between M_3 and the mandibular articulation; M1M3, length of the lower molar series; P2P4, length of the lower premolar series; C-P2, length of the diastema (distance measured between the lower canine and P_2).

Figure 14. Reconstruction of the angle between the hemi-mandibles of *Megaceroides algericus* (Lydekker, 1890) based on the specimen FIL166 (MNMH). The arrows indicate the direction of the wearing traces caused by coarse forage.
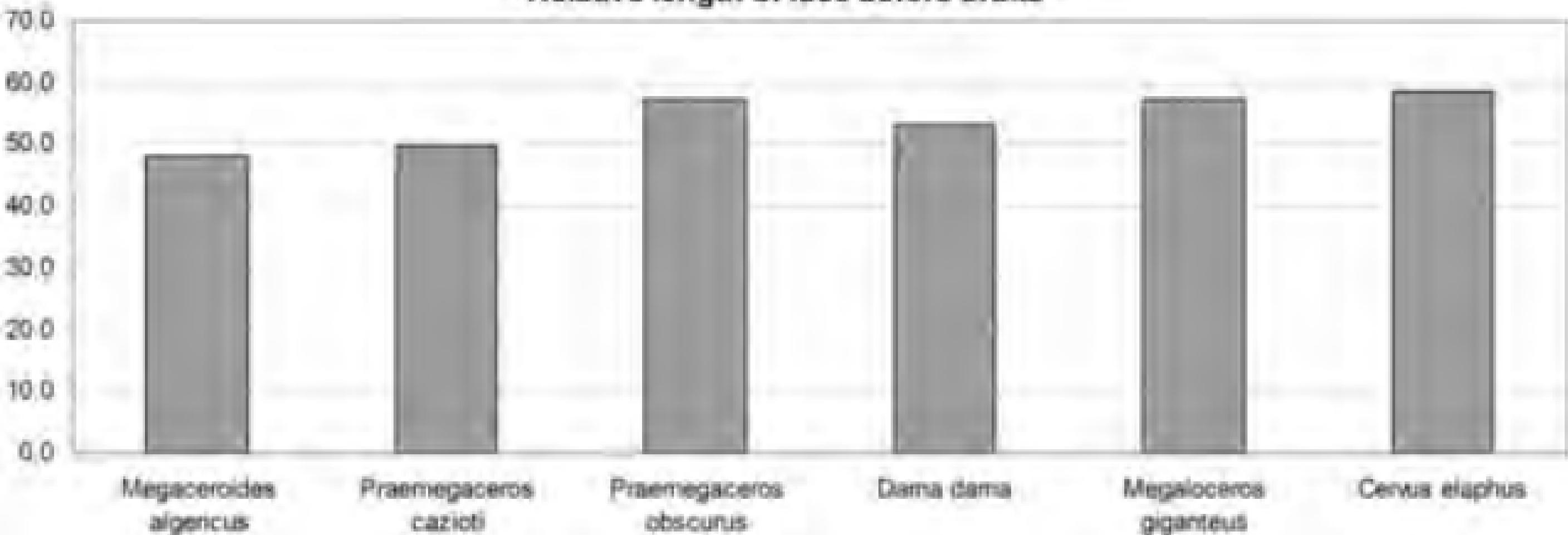
Figure 15. Comparison of antler morphology of giant cervids and their endemic small-sized relatives. **A**. *Megaceroides algericus* (Allo. 61.12) from the late Pleistocene of Phacochères (Algeria; reversed image adapted from Hadjiouis, 1990). **B**. *Megaloceros giganteus* from Lough Gur, Limerick (Ireland; adapted from Reynolds, 1929). **C**. *Praemegaceros dawkinsi* from the middle Pleistocene of Mundesley, Norfolk (Great Britain; M18706, NHML, reversed). **D**. *Praemegaceros obscurus* from the early Pleistocene of Salcia (Moldova, Institute of Zoology of the Academy of Sciences of Moldova, no number). *b.*, basal tine; *sb.*, sub-basal tine; *ds.*, dorsal tine; *m.*, middle tine; *p.*, posterior tine; *cr.*, crown tine; *pl.*, palmation. Scale bars: 10 cm.
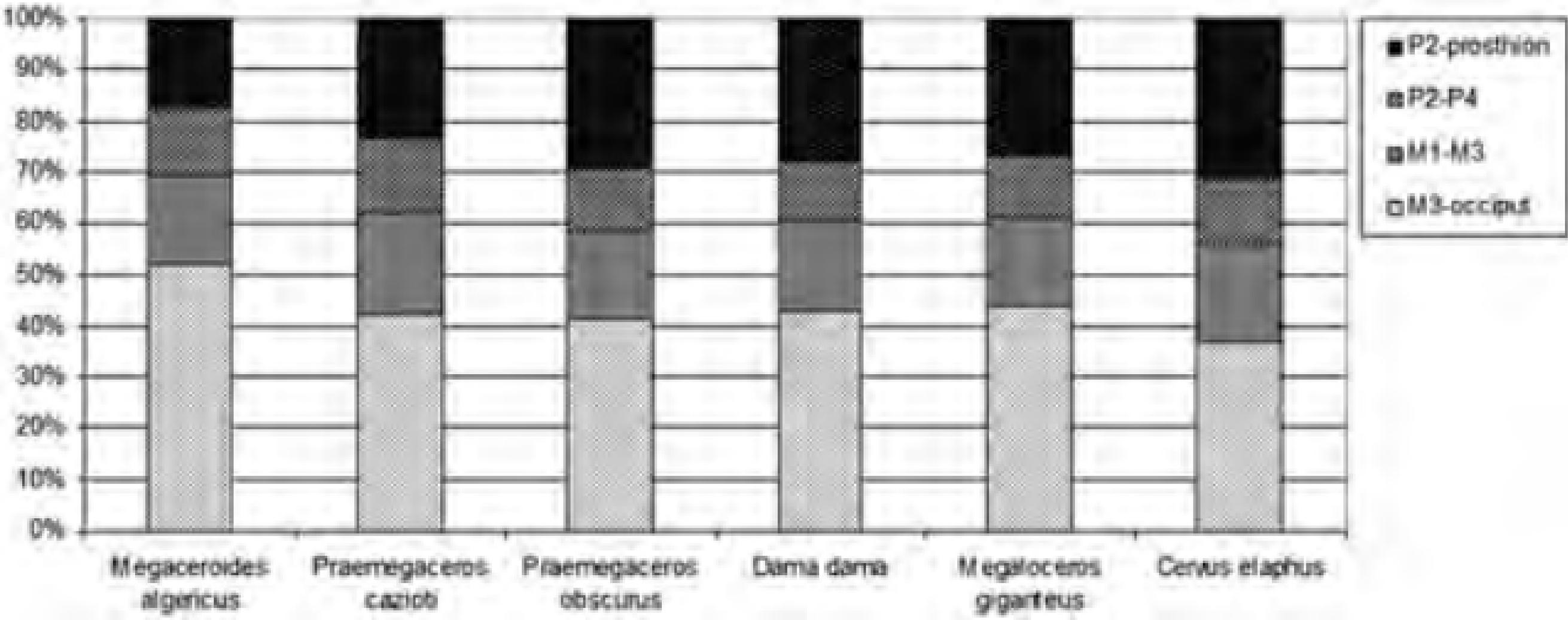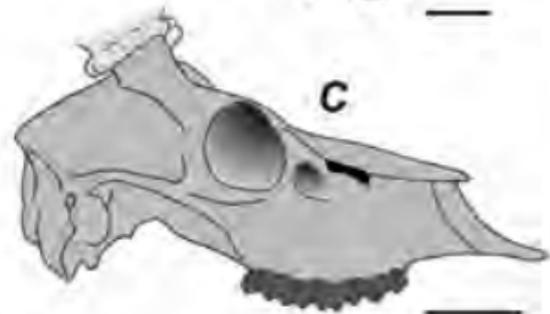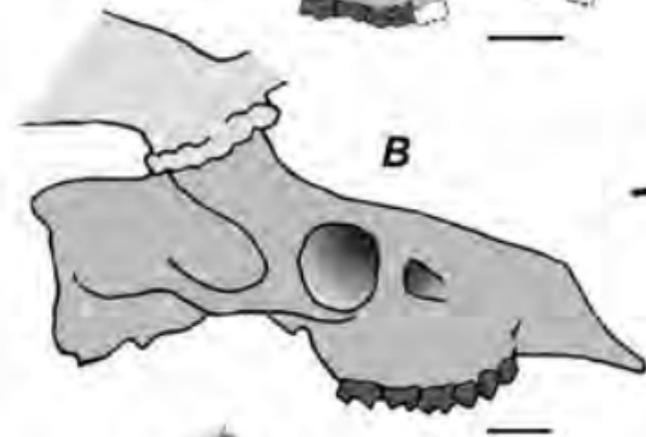
Relative length of face before orbits

Chart showing values for:
- Megaceroides algericus
- Praemegaceros cazioti
- Praemegaceros obscurus
- Dama dama
- Megaloceros giganteus
- Cervus elaphus

Y-axis ranges from 0.0 to 70.0

Legend:
- P2-prosthion
- P2-P4
- M1-M3
- M3-occiput

Categories (x-axis): Megaceroides algericus, Praemegaceros cazioti, Praemegaceros obscurus, Dama dama, Megaloceros giganteus, Cervus elaphus

A 135°

B 155°

C 128°

A

B

nas.

M^2 M^3

37°

A

B

15.4 mm
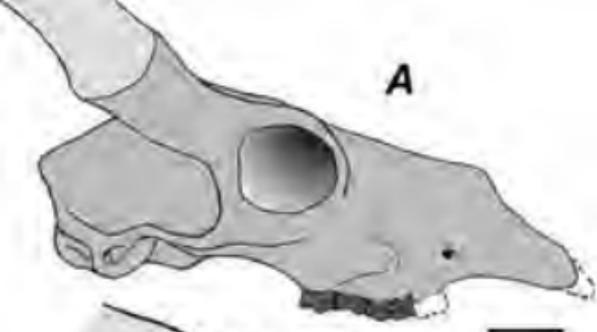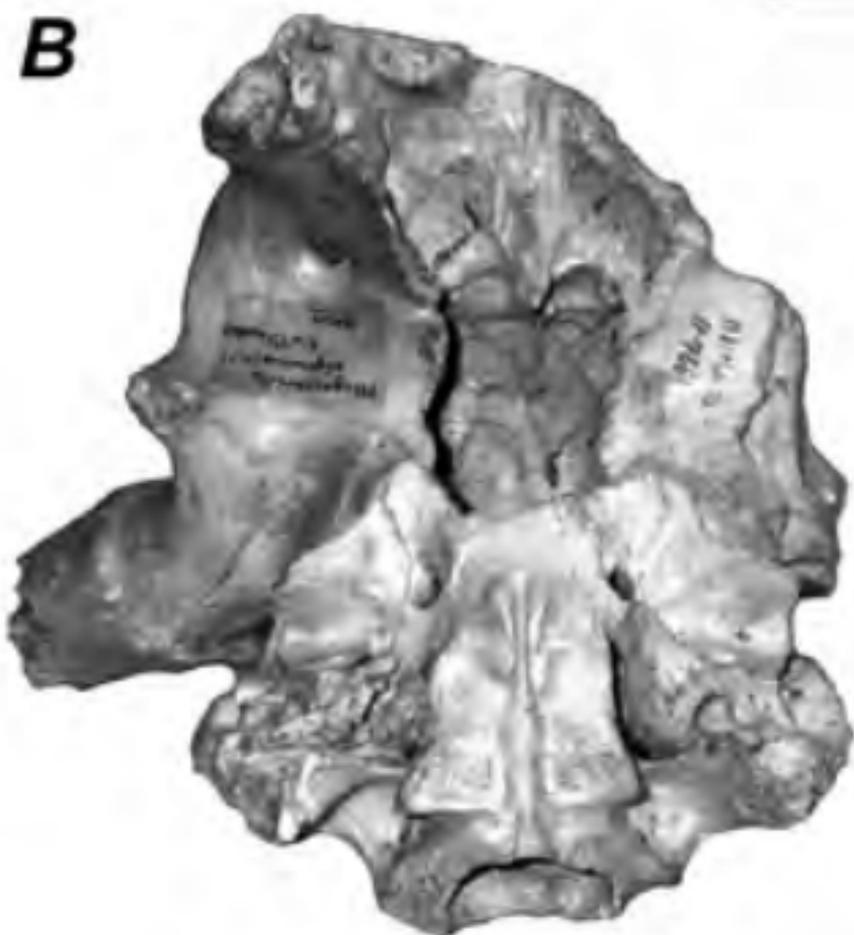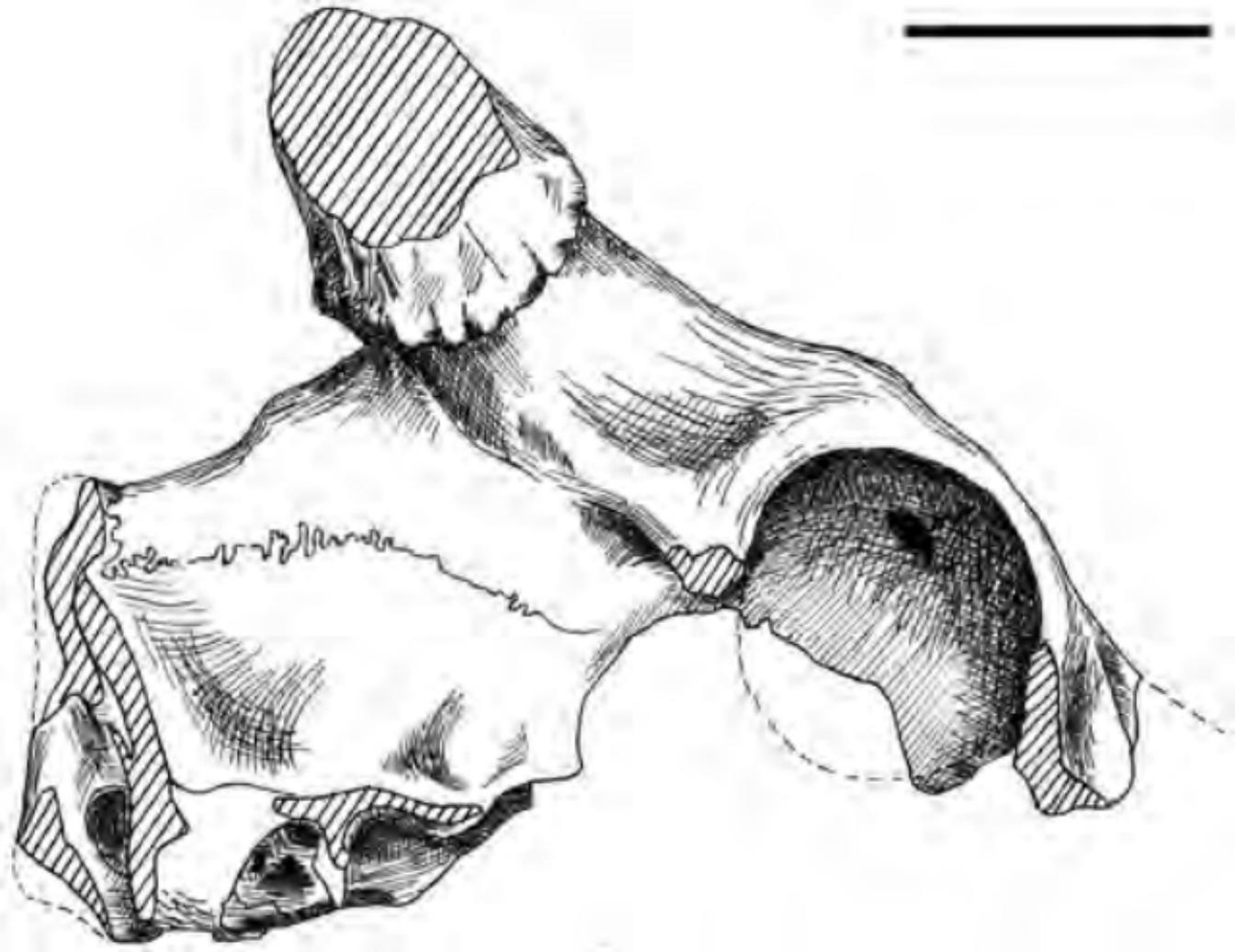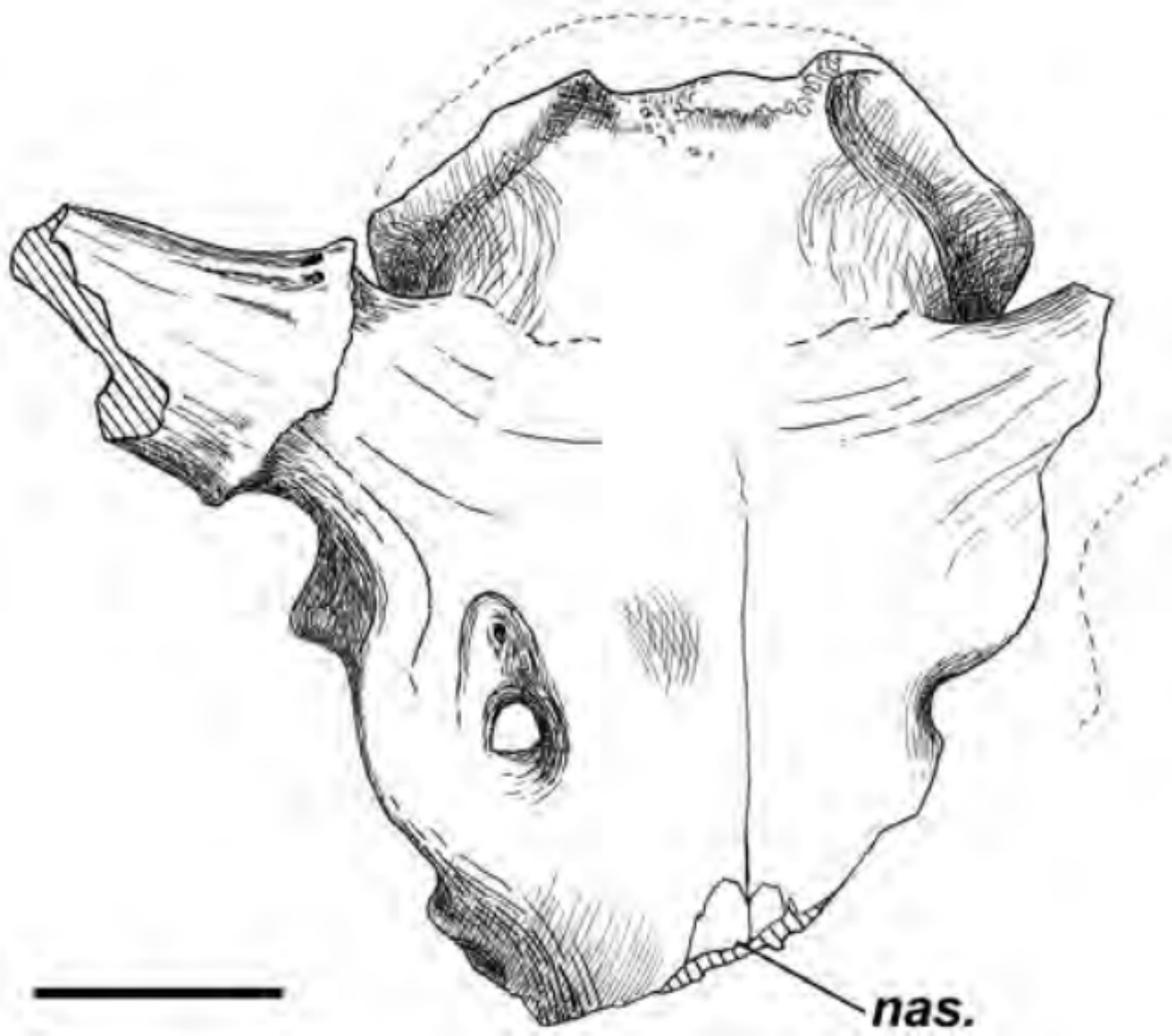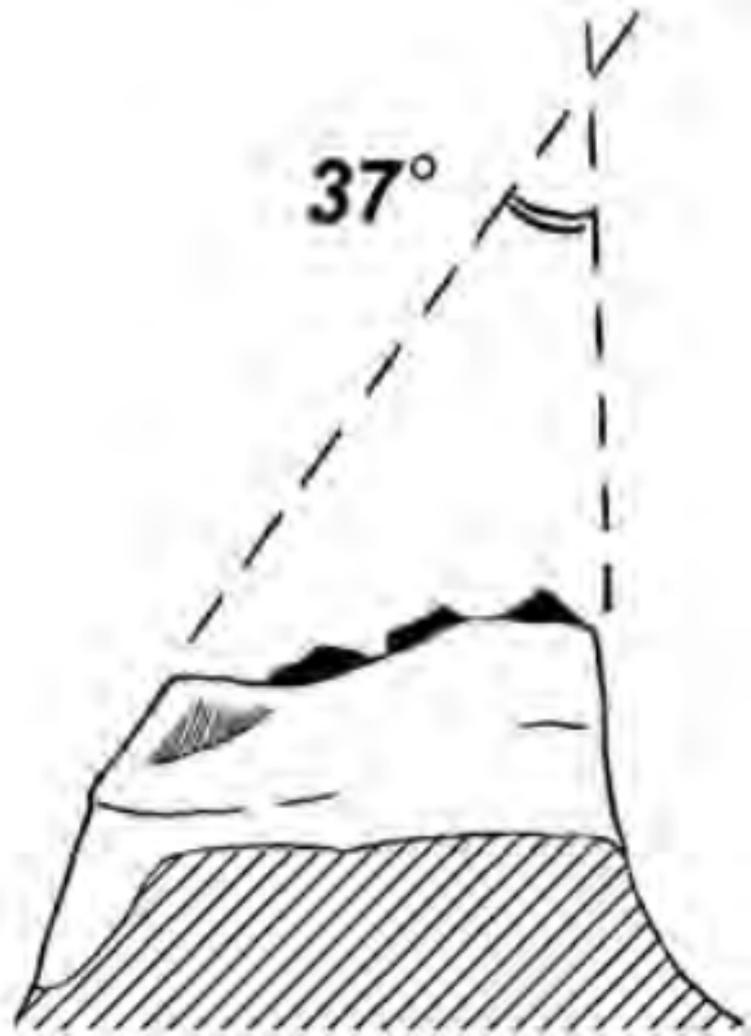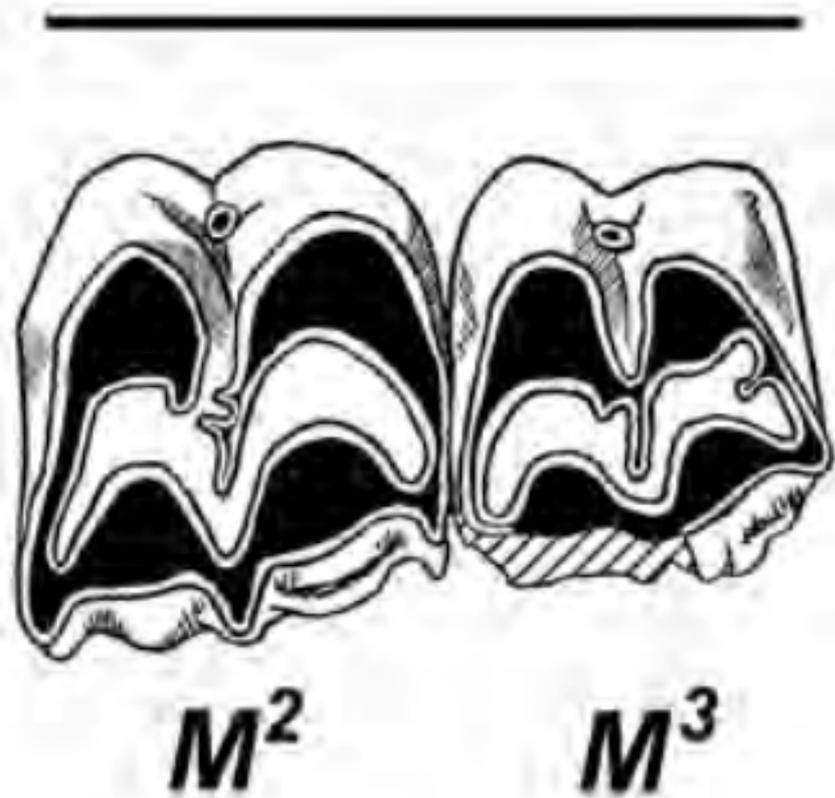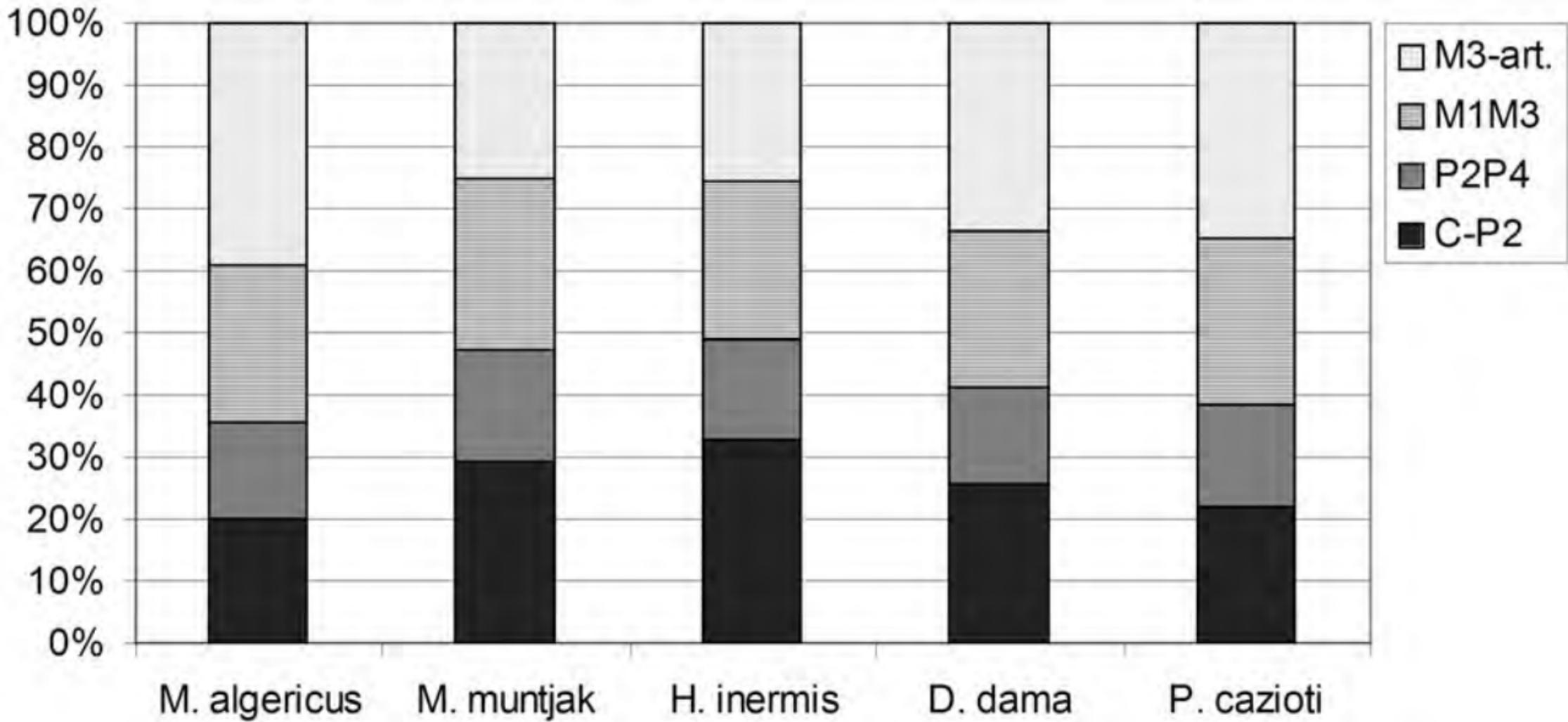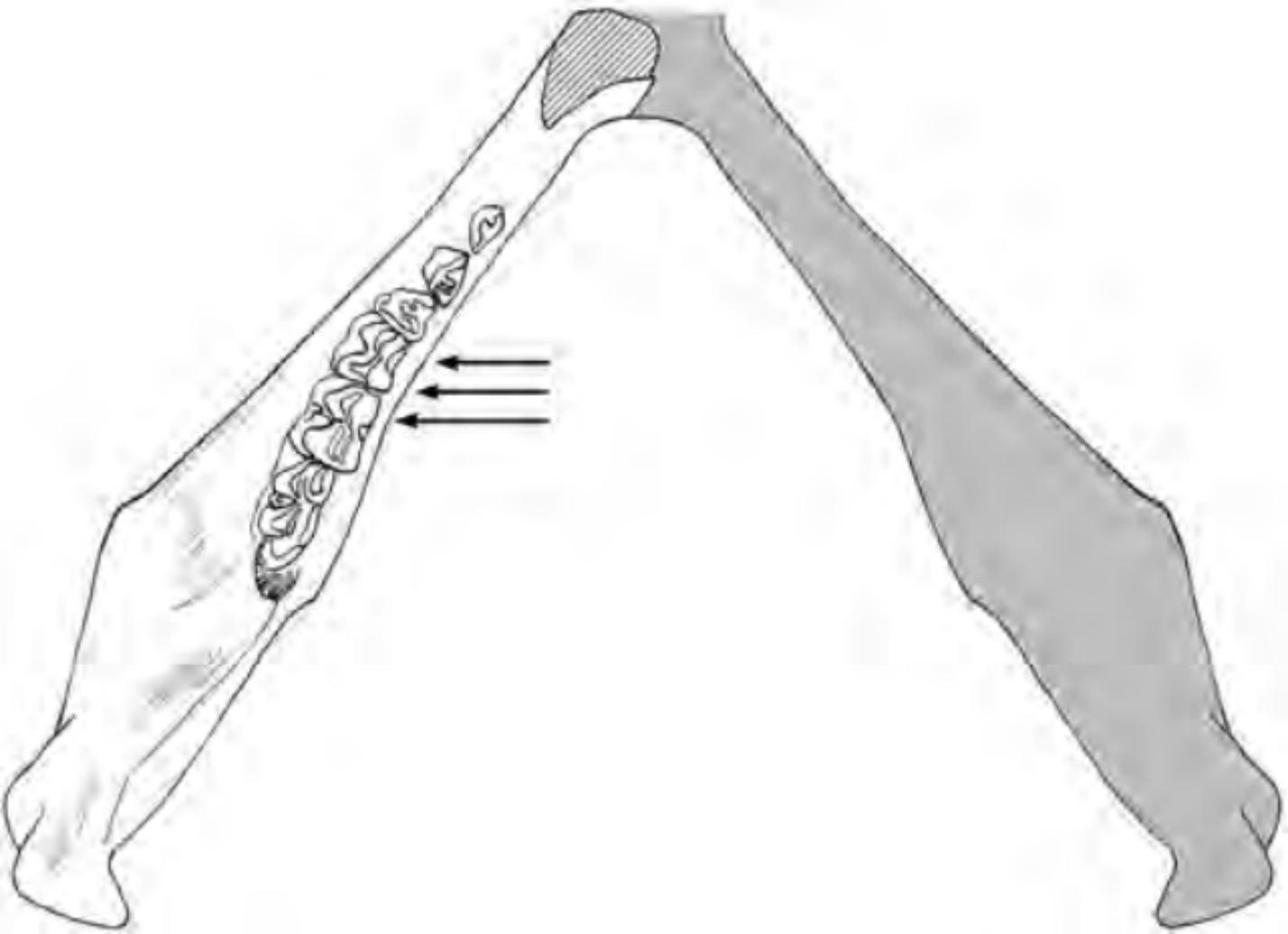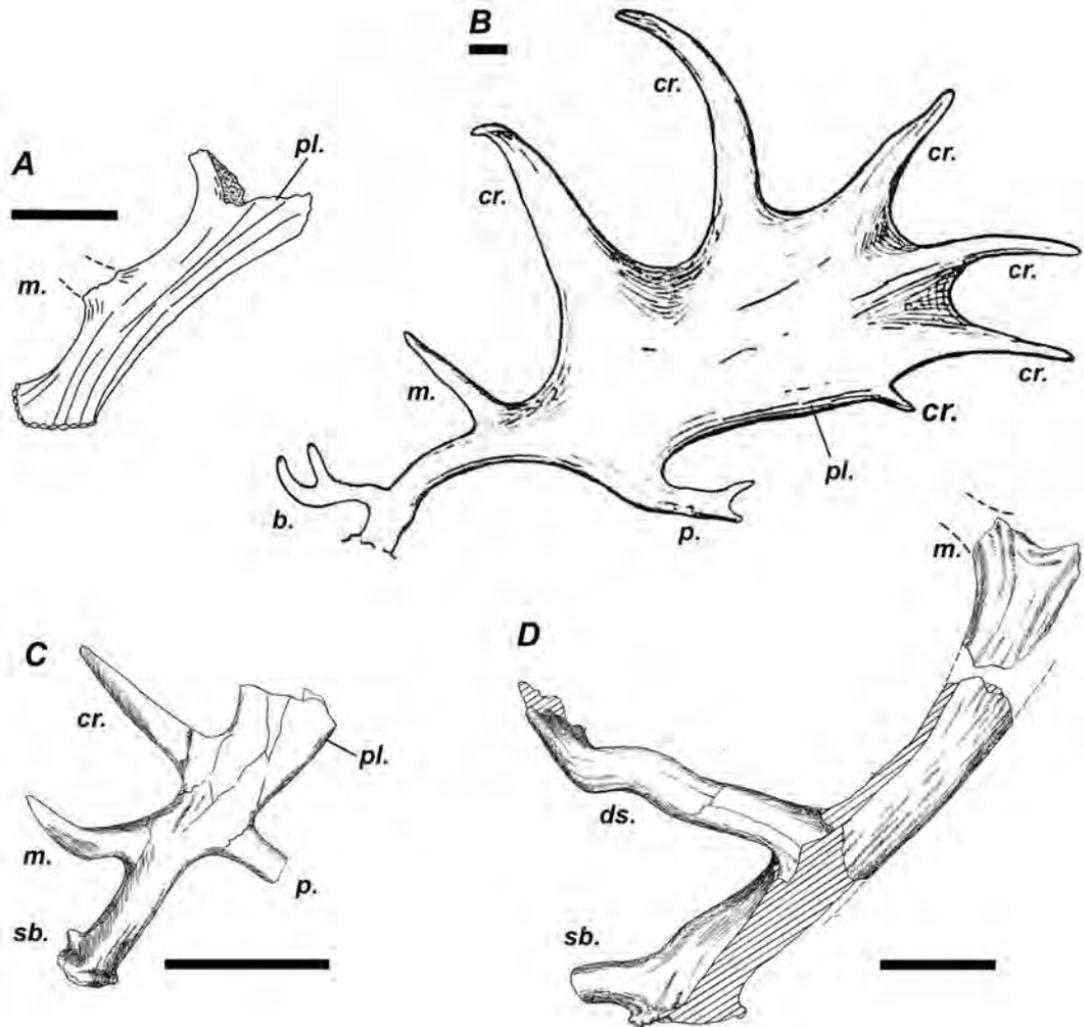
Table 1.

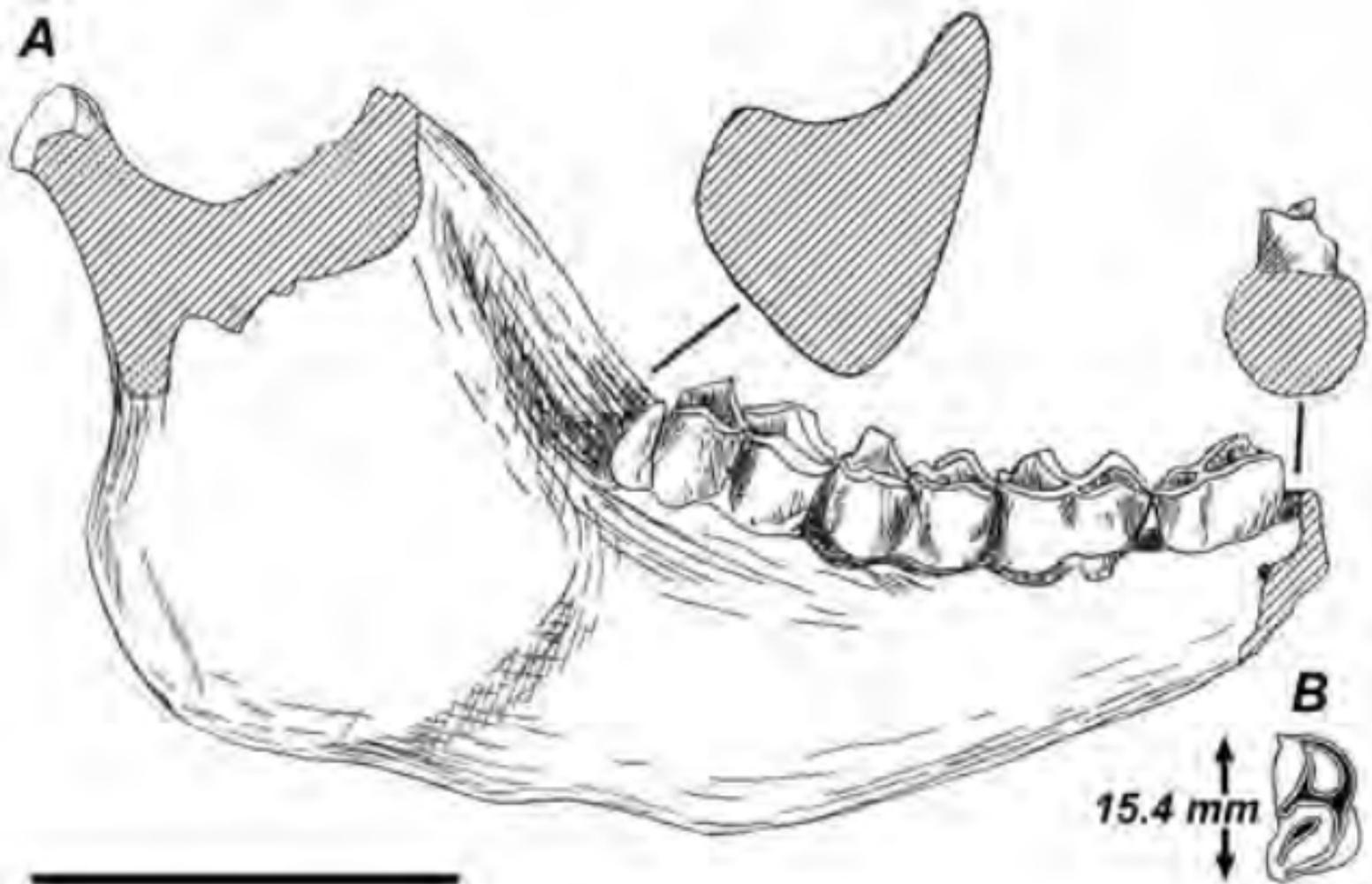| Collection number and additional information	Specimen	Site	Original citation
No number; labeled as "*Cervus algericus*, figuré: pl. IV, fig. 4", no bibliographic reference; indicated as GM/1 in this work	Right hemimandible with P_4-M_3	Grotte de la Madeleine	Described in Croitor (2006: fig. 2 A-B, p. 94) as *Megaceroides algericus* (Lydekker)
No number; indicated as GM/2 in this work	Hemimandible with M_2-M_3, showing a pathologic malformation on processus angularis	Grotte de la Madeleine	unpublished
No number, "Collection of Arambourg"; indicated as the "skull from Guyotville" in this work	Almost complete skull with proximal parts of antlers	Guyotville	*Cervus* (*Megaceroides*) *algericus* Lydekker (Arambourg, 1932: fig. 3, p. 137)
Nr. 336, "Collection of Arambourg"	Left hemimendible with M_2 and M_3	Guyotville	unpublished
Nr. 337, "Collection of Arambourg"	Left hemimandible with P_4-M_3	Guyotville	unpublished
MOC148, "Mission Arambourg"	Damaged neurocranium with frontal bones and a right basal part of antler	Ain Tit Mellil	*Cervus* (*Megaceroides*) *algericus* Lydekker (Arambourg, 1938: pl. II, figs. 2, 2a)
Fil-160	Juvenile hemimandible	Filfila	unpublished
Fil-166	Left complete hemimandible with P_2-M_3	Filfila	*Megaceroides algericus* (Lydekker) (Thomas, 1979; figured)
Fil-167	Fragment of hemimandible with M_2 and M_3	Filfila	unpublished
Fil-169	Right maxilla with M^2 and M^3	Filfila	unpublished
No number; indicated as Fil/nn in this work	Fragment of mandible with P_4	Filfila	unpublished

Table 2.

Species	Source/collection	CBL	P^2-M^3	M^3oc	M^1-M^3	P^2-P^4	P^2pr.	or-pr.	Dor.	or-oc.
Praemegaceros cazioti	Caloi and Malatesta (1974)	300.0	101.0	132.7	62.0	45.0	73.5	149.0	44.0	-
Praemegaceros obscurus	IGF4024, Croitor (2014)	470.0	141.8	200.0	84.0	61.3	143.0	270.0	-	140.0
Dama dama	47.1.1.4 (NHML)	270.0	77.0	116.8	47.8	31.0	77.0	144.0	52.8	93.0
Dama dama	c.12058 (ZMS)	270.0	81.7	112.8	49.8	34.2	76.0	145.7	42.8	84.7
Megaloceros giganteus	M28968 (NHML)	505.0	150.0	223.0	90.0	60.0	137.4	290.0	56.1	185.2
Cervus elaphus	1927-58 (MNHN)	353.0	109.8	131.4	68.7	45.2	111.8	207.0	-	-

Table 3.

Species	Source/collection	C-P_2	P_2-P_4	M_1-M_3	M_3-art.	gn.-M_1	M_1-art.	art.-gn.
Muntiacus muntjak	c.780 (ZMS)	40.0	24.5	38.0	34.4	67.3	64.3	135.6
Hydropotes inermis	c.1441 (ZMS)	42.0	20.2	32.3	32.8	70.3	57.1	126.4
Dama dama	c.12061 (ZMS)	56.5	34.3	56.0	73.7	105.0	120.0	222.0
Praemegaceros cazioti	COS19040, Croitor et al. (2006)	50.4	37.6	62.0	80.0	115.0	126.2	235.0

Table 4.

Measurements (in mm)	Guyotville =Ain-Benian (Algeria)	MOC-148, Ain Tit Mellil (Maroc)
Condylo-basal length	~310	-
Distance between occiput and P^2	~255	-
Upper cheek teeth length, P^2-M^3 (sin.)	91.4	-
Upper premolar series length (sin.)	42.6	-
Upper molar series length (sin.)	54.1	-
Maximal breadth of skull (at orbits)	193.3	-
Bread of forehead begind orbits	177.8	-
Antero-posterior diameter of orbit (dx.)	57.8	-
Distance between occiput and orbit	122.5	-
Distance between orbit and prosthion	~150	-
Breadth of muzzle	81.8	-
Distance prosthion-nasion	~155	-
Distance nasion-bregma	114.0	107.0
Distance prosthion-bregma	~290	-
Distance bregma-opistocranion	~85	83.0
Breadth of braincase behind pedicles	121.7	116.3
Height of occiput	-	86.0
Breadth of occiput	~162	146.7
Breadth of occipital condyles	-	68.3
Diameter of pedicle (DV×LM; dx. / sin.)	46.3×55.5 / 48.3×50.0	44.0×49.3 / -×-
Palatal breadth between PP^4	65.1	-
Palatal breadth between MM^3	68.4	-

Table 5.

Tooth measurements (mm)		Guyotville (no number)		Filfila (FIL169)
		sin.	dx.	dx.
P^4	length	13.8	13.6	-
	breadth	19.1	19.0	-
M^1	length	17.8	18.7	-
	breadth	19.4	20.7	-
M^2	length	19.5	19.7	17.8
	breadth	21.6	22.2	21.3
M^3	length	18.9	18.7	16.1
	breadth	20.8	21.0	18.2

Table 6.

Measurements	FIL166 sin.	GM/1 dx.	GM/2 dx.	GTV337 sin.	GTV336 sin.	FIL167	FIL160
L P_2-M_3	95.2	-	-	-	-	-	-
L P_2-P_4	35.0	-	-	-	-	-	-
L M_1-M_3	57.5	65.8	-	61.6	-	-	-
L M_2-M_3	42.1	45.2	41.0	42.8	46.0	43.7	-
L horizontal ramus	215$^+$	-	-	-	-	-	-
L diastema	45$^+$	-	-	-	-	-	-
L P_2 - foramen mentale	20.3	-	-	-	-	-	-
H at ½ diastema	20.0	-	-	-	-	-	-
H under P_2	18.7	-	-	-	-	-	-
D under P_2	15.4	-	-	-	-	-	-
H under M_1	21.5	19.0	20.3	19.8	-	-	-
D under M_1	21.8	22.8	-	20.4	-	21.2	19.0
H under M_2/M_3	30.8	34.6	33.4	-	35.0	34.3	32.5
D under M_2/M_3	27.6	31.1	33.8	29.3	32.1	29.2	23.0
D maximal	37.2	34.3	35.5	36.3	39.0	36.2	-
H ascending ramus	100.6	-	96.0	108.4	109.2	-	-
L articulation - gnation	230.0	-	-	-	-	-	-
L articulation - M_3	88.3	75.2	-	-	92.7	84.5	-

Table 7.

Tooth measurements		Fil-166	Fil-167	Fil/nn	GM/1	GM/2	Nr.336	Nr.337	Pomel (1892)
P_3	L	13.8	-	-	-	-	-	-	-
	D	9.3	-	-	-	-	-	-	-
P_4	L	13.1	-	13.6	15.5	-	-	13.7	-
	D	11.4	-	10.2	11.7	-	-	10.4	-
M_1	L	18.2	-	-	17.2	-	-	19.2	-
	D	14.3	-	-	13.9	-	-	14.0	-
M_2	L	18.4	19.2	-	19.8	18.0	20.2	19.0	20.0
	D	13.8	14.0	-	15.0	14.1	14.0	12.9	15.0
M_3	L	23.9	24.1	-	23.0	23.0	25.8	23.0	22.0
	D	11.7	11.7	-	13.2	12.1	14.0	12.4	10.0

Table 8.

Characters	*Megaceroides algericus*	*Megaloceros giganteus*	*Dama dama*
1. Length of face before orbits	quite short (48.4% of CBL)	relatively long (57.4% of CBL)	moderately short (53.3% of CBL)
2. Relative breadth of skull	62.4% of CBL	39.6-43.1% of CBL	35.7-41.9% of CBL
3. Angle between axes of face and braincase	135º (moderately flexed neurocranium)	155º (little flexed neurocranium)	120º (flexed neurocranium)
4. Relative size of orbits	relatively large (18.6% of CBL)	relatively small (11.1% of CBL)	relatively large (19.6% of CBL)
5. Development of pachyostosis	Pachyostosis of cranial bones and lower mandible strongly developed	Pachyostosis of cranial bones and lower mandible strongly developed	No pachyostosis
6. Shape of parietal bones	Flattened parietal bones	Flattened parietal bones	Convex parietal bones
7. Shape of frontal bones	Flattened frontal bones	Concave frontal bones	Convex frontal bones
8. orientation of pedicles	Pedicles deflected caudally and sideward	Pedicles deflected caudally and sideward	Vertically oriented pedicles
9. Position of nasal bones	Posterior edge of nasal bones extends behind the anterior line of orbits	Posterior edge of nasal bones extends behind the anterior line of orbits	Posterior edge of nasal bones extends behind the anterior line of orbits
10. Position of orbits.	Anterior edge of orbit situated above M^2	Anterior edge of orbit situated above M^3	Anterior edge of orbit situated above M^2
11. Length of naso-premaxillary suture	Naso-premaxillary suture is long	Naso-premaxillary suture is long	Naso-premaxillary suture is short
12. Development of preorbital fossae	reduced	reduced or well-developed	well-developed
13. Development of ethmoidal orifice	closed	reduced or completely closed	very large
14. Size and shape of bulla tympani	rather large and rounded	intermediate size	very large and rounded
15. Shape of mandible	Ascending part of mandible is sloped backward	Ascending part of mandible is set vertically	Ascending part of mandible is set vertically
16. Development of cingulum	A variing cingulum is present	A variing cingulum is present	No cingulum
17. Angle between lingual and labial sides of M^2	37º	45º	37º
18. Development of upper canines	missing	missing	missing
19. Position of upper tooth row	displaced orally	in normal position	in normal position