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Original article

The morphological distinction between the postcranial skeleton of *Cervalces/Alces* and *Megaloceros giganteus* and comparison between the two Alceini genera from the Upper Pliocene–Holocene of Western Europe

Distinction morphologique entre le squelette postcrânien de *Cervalces/Alces* et celui de *Megaloceros giganteus* et confrontation entre les deux genres d'Alcines du Pliocène supérieur–Holocène d'Europe Occidentale

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Abstract

Alces alces, *Cervalces* and *Megaloceros giganteus* are deer of approximately the same size whose limb bones could be exchanged if fragmentary so morphological features are needed, enabling identification of postcranial remains. In this work the limb bone features described by Pfeiffer (1999a) as distinguishing *Cervalces latifrons* from *M. giganteus* are re-analyzed and further developed, considering also the vertebral column, the articular girdles and the carpals and tarsal elements. This analysis is extended to the other *Cervalces* species (*C. gallicus*, *C. carnutorum* and *C. scotti*) and to the present-day moose *Alces alces*. It results in a substantial uniformity in the postcranial skeleton of the species of the genus *Cervalces*, confirming what has already been stated by Sher (1987), that the Alceini, in the Upper Pliocene, constituted an already well-defined morphological type that did not undergo further structural postcranial remodeling.

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Résumé

Alces alces, *Cervalces* et *Megaloceros giganteus* sont des cerfs de la même taille dont les os des membres peuvent être confondus si fragmentés, en conséquence, il faut avoir des caractères morphologiques qui permettent la détermination des restes postcrâniens. Par ce travail on a réexaminé et considérablement enrichi les caractères des os des membres décrits par Pfeiffer (1999a) comme distinctifs entre *Cervalces latifrons* et *M. giganteus* en prenant en considération aussi la colonne vertébrale, les ceintures articulaires et les éléments du carpe et tarse. Cette analyse s'étend aux autres espèces du genre *Cervalces* (*C. gallicus*, *C. carnutorum* et *C. scotti*) et à l'élan actuel *A. alces*. Il ressort une substantielle uniformité des squelettes postcrâniens des espèces de *Cervalces*, ce qui confirme ce que Sher (1987) avait déjà suggéré, c'est-à-dire que, au Pliocène supérieur, les Alcines constituaient un type morphologique déjà bien défini qui n'aurait ensuite subi aucune transformation structurelle postcrânienne.

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Keywords: *Cervalces*; *Alces alces*; *Megaloceros giganteus*; Postcranial skeleton; Morphological features

Mots clés : *Cervalces* ; *Alces alces* ; *Megaloceros giganteus* ; Squelette postcrânien ; Caractères morphologiques

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1. Introduction

Usually, the deer systematics is solely based on antler and cranial morphology, and many authors do not take limb bone morphology into account, assigning postcranial remains to the species of that size present in the site. However morphological identification is necessary for all the isolated postcranial remains of alluvial origin or without a stratigraphic position, whose identification has to prescind from the geological age.

Among the large deer, the Alceini tribe (both the living *Alces* Gray, 1821 and the extinct *Cervalces* Scott, 1885) is about the same size as *Megaloceros giganteus* (Blumenbach, 1799). Complete long bones are easy to identify because those of the moose are longer and slender in proportion. Pfeiffer (1999a) observes that for remains consisting of only the proximal or distal portion there is a dimensional superposition between the epiphyses of the two animals. The German researcher describes the morphology of the long bones of the two large deer in detail, in order to find morphological criteria of identification for fragmentary limb bones remains.

In the present work, the morphological distinctions found by Pfeiffer (1999a) between the giant deer and the broad fronted moose are reviewed and further developed. Moreover the postcranial differences among the various species of the genus *Cervalces* and the genus *Alces*, represented only by the living species *A. alces* (Linnaeus, 1758), are taken into account here. *Alces* can be differentiated from *Cervalces* in some cranial features, i.e. the tall and narrow occipital and the short nasals not articulated to the long premaxillaries (Scott, 1885; Azzaroli, 1952, 1982, 1985, 1994; Breda, 2001), or in the antlers structure (Breda unpublished; Breda and Marchetti, 2005). On the contrary, the various species of the genus *Cervalces*, *C. gallicus* (Azzaroli, 1952), *C. latifrons* (Johnson, 1874) and the doubtful *C. carnutorum* (Laugel, 1862), do not show proper features allowing for specific identification on morphological grounds alone, but dimensional data are required (Breda, unpublished). In fact, there is a size increase from *C. gallicus* of the Middle and Upper Villafranchian, through the intermediate *C. carnutorum*, till the huge *C. latifrons* of the Middle and early Late Pleistocene (Lister, 1993a; Lister, 1993b in Martin and Barnosky). They are usually considered “chronospecies” of the same phyletic line, which underwent an “anagenetic” evolution towards a body mass increment, following, in this regard, the well-known rule of Cope. Lister (1993a) points that with so few chronological sampling points, it is impossible to say if the transition was gradualistic (anagenetic) or punctuated (cladogenetic).

The Alceini, in comparison to the Megacerini and to other deer in general, seem to have a lower sexual dimorphism. In *M. giganteus* there is, in fact, a wider dimensional range in the single bone elements that, in some of them (e.g. the radii), involve the identification of two size classes (in this case, the dimensional difference lies more in the diaphysis breadth than in the full bone length). On the contrary, the sexual dimorphism is reduced in living moose (Franzmann et al., 1978),

perhaps because of their different social structure, lacking a dominant male leading a female harem (Geist, 1999). The adult bull lives alone and fights other males to conquer the single female and not for a seasonal role of herd leading, as in the other Old World deer, Megacerines included (Geist, 1999). The same ethology can be inferred for the genus *Cervalces*, because its remains, even if distributed in a wide geographical range, are always scanty in comparison with those of other Quaternary ungulates (Sher, 1987). Consequently, the sexual dimorphism, should have been low in *Cervalces* as in living *Alces* (Breda, unpublished).

2. Materials and methods

The present analysis was possible thanks to the rich fossil collection of the Naturhistorisches Museum of Mainz (NHMM, in the text) (Rheinland Pfalz, Germany). Its many postcranial skeleton elements of *C. latifrons*/*C. carnutorum* and of *M. giganteus* enabled direct comparison between the same skeleton elements of the two genera.

The *Cervalces* remains stored in Mainz come from Mosbach (Wiesbaden Biebrich, Germany) that yielded by far the most abundant remains of this genus in Europe. These remains cannot be used in a metrical comparison because the bones were collected without their horizon of origin being recorded. Thus they cannot be attributed definitively to the two stratigraphical levels: Mosbach 1 from the end of Lower Pleistocene and Mosbach 2 from the early Middle Pleistocene, respectively, with *C. carnutorum* and *C. latifrons* (Kahlke, 1960; Breda, unpublished; Breda and Marchetti, 2005) even if the large majority of Mosbach remains are from Mosbach 2. The moose remains from Mosbach are of definite generic identification because the only other large sized artiodactyl is bison. So, the first phase of the analysis consisted in verifying the identifications through the features described by Heintz (1970) as distinguishing Bovids and Cervids.

The *M. giganteus* remains come from many Upper Pleistocene places of the upper Rhine Valley (Eich Buttel, Gimbshheim, Geinsheim, ecc). Because these localities yielded *A. alces* and, following Koenigswald and Menger (1997) *C. latifrons* remains as well, only the complete bones were used in comparison, as their identification was in no doubt. The plentiful remains from the upper Rhine Valley and their excellent state of preservation meant more samples were available for any long bone element, avoiding considering individual features. The giant deer features were later verified also in the rich collection from Ireland, kept in the Natural History Museum of London (NHML, in the text) which was used for those elements, as axis, carpals and tarsals not present in the Mainz collection.

As for *A. alces*, seven complete skeletons were used in comparison: one stored in the NHMM (1961/1) belonging to an adult male of unknown origin; one kindly lent by the Archaeology and Arts History Department, University of Siena (UniSI, in the text), which belonged to an animal from

a zoo in Italy; one of a young Norwegian male, of approximately definitive size, expressly prepared by the author and now stored in the Natural and Cultural Resources Department, University of Ferrara (UniFE in the text), one adult male from Prussia (H.17.691) stored in the University Museum of Zoology of Cambridge (UMZC, in the text), and three specimens stored in the osteological collection of the NHML, precisely a young female (1851.11.10.03), a young male (1850.11.22.72), an adult male (1851.6.4.1). The different age of the specimens was useful in analyzing all those features, as development of all the muscular insertion surfaces, which depend on the sex and the age of the animal. The features were tested also on the *A. alces* remains from the early Holocene site of Starr Carr (Yorkshire, UK), in the NHML, which comprehend many postcranials.

The features observed in the *Cervalces* samples from Mosbach were later verified, through photographic comparison, in the *C. gallicus* holotype from Sènèze (Azzaroli, 1952; Breda, 2001; in the Musée Géologique de l'Université Claude Bernard Lyon-1), in the *C. carnutorum* remains from Untermassfeld [Kahlke, 1997; in the Institut für Quartärpaläontologie, Weimar (IQW in the text)], in the *C. latifrons* remains from the English Forest Bed (Azzaroli, 1953, 1994; Lister, 1993c; in the NHML and in the Norwich Castle Museum) and from many German localities [Voigtstedt (Kahlke, 1965; in the IQW), Bilshausen (Schmidt, 1934; in the Museum für Geologie und Paläontologie, Göttingen), Süßenborn (Kahlke, 1969; in the IQW), Mauer (Soergel, 1914; in the Staatliches Museum für Naturkunde, Karlsruhe), Ehringsdorf (Kahlke, 1975; in the IQW)] and in the *C. scotti* holotype from New Jersey (Scott, 1885; in New Jersey State Museum, Trenton).

Pfeiffer's work (1999a) has been a guide in the analysis of *Cervalces/M. giganteus* differences and the description will make reference to it confirming or denying its features. The number of each of Pfeiffer's feature has been maintained (unless explicitly indicated to the contrary) both in the text and in the figures, to facilitate comparison (if necessary) and the new features are marked with progressive numbering. The present analysis also deals with the atlas, the axis, the articular girdles and the carpal and tarsal elements not been considered by the German writer.

As for the *Cervalces/A. alces* differences, the only authors to study the morphology of the postcranial skeleton of *Cervalces* were Sher (1974), only for the ulna and the metatarsal bone, and Scott (1885), for the whole skeleton of the North American type species *C. scotti*. The observations by Scott, who had at his disposal a complete and wonderfully kept skeleton from New Jersey, preserving even the cartilaginous portions, are far more subtle than what is possible with the isolated and usually fragmented bones of the European species. Statements by Scott have been reported here, while awaiting confirmation by a better European fossil record.

The von den Driesch (1976) directional nomenclature was followed in the morphological descriptions. The linear black scales in the line-drawings are better referred to *M. giganteus* because of the wide size range in the *Alces/Cervalces* species.

3. Morphological features useful in the identification of postcranial skeleton remains

3.1. Vertebral column

Azzaroli (1952) in describing the *C. gallicus* holotype from Sènèze states that *Cervalces* had a longer neck than present-day *Alces*. But this specimen consists of a mounted skeleton in which the cervical vertebrae are badly assembled: too far apart from one another and lined up on a nearly vertical axis, increasing the length of the neck and giving to the head a more Cervine than Alcine set. Moreover, some vertebrae do not belong to the same specimen, because the articular surfaces of vertebral bodies are not fused, indicating a young age in contrast with the more advanced one attested to by the worn teeth and bone morphology in general (Breda, 2001). Scott (1885) had already stated that the neck of the *C. scotti* from New Jersey (in far better condition and so more reliable than the damaged French skeleton) was shorter than the *A. alces*.

M. giganteus, in comparison with *Alces* and *Cervalces*, possesses a longer neck with stronger vertebrae and with all the processes more developed. The trunk, too, is shorter in *Alces/Cervalces* because all the vertebral bodies are shorter and do not have the long, strong spinosus process present in the giant deer (Scott, 1885). Probably *Cervalces*, because of its short neck, had fewer problems than *M. giganteus* in supporting the head with the massive antlers.

3.1.1. Atlas

The atlas is the only vertebra of sure identification among the Mosbach material. Scott (1885) suggests that the *Cervalces* atlas posses a stronger ipoapophysis (or ventral tubercle) than the *Alces*. But the ipoapophysis is well developed in *Alces* as well (Fig. 1(1)) and, as in *Cervalces*, constitutes a different center of ossification that joins the ventral arch very late, so that often the apophysis is lost and the surface of the epiphyseal cartilage is visible. On the contrary the atlas lacks the ipoapophysis in *M. giganteus*.

The cranio-ventral edge of the articular surfaces to the occipital condyles, in ventral view, in the moose has an indentation in the middle (Fig. 1(2)) that is lacking in the giant deer.

The shape of the transverse processes also differ: in the giant deer the edges of the wings are always thick and caudally divergent, extending into two large tubercles that form a small angle with the articular surface to the axis (Fig. 1(3)). In the moose, the edges of the wings are thin (sometimes sharp), more parallel one to each other, extending in smaller caudal tubercles (sometimes with sharp and dorsally bent edges). The development of the wings, always strong in the giant deer, is variable in the Alceini tribe: *Cervalces* is closer than *A. alces* to the morphology of *M. giganteus* having edges more thick and diverging in larger caudal tubercles. Within *A. alces*, adult males have stronger wings than young individuals and females. The first cervical vertebra, in fact, clearly

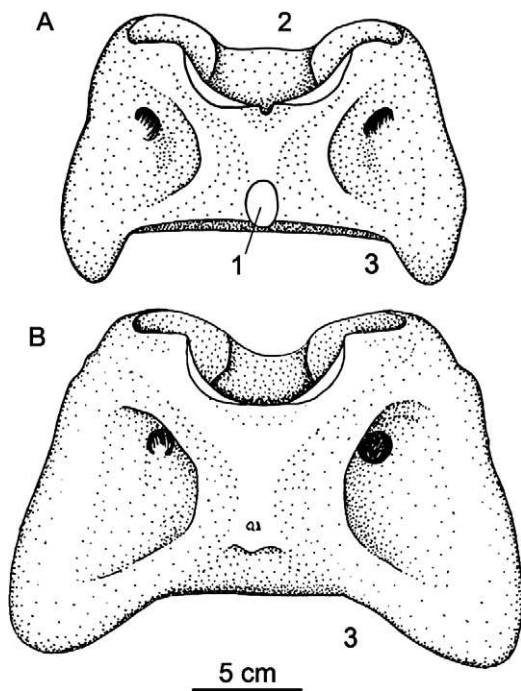


Fig. 1. Atlas, ventral view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 1. Atlas, vue ventrale.

reflects the difference in head weight due to the antlers and so it may show a stronger sexual dimorphism than other body portions. Actually, there is a wide size range in the *Cervalces* atlas from Mosbach. The smaller atlases are of about the same size as in *P. verticornis* from the same site and as in present-day *A. alces*. Nevertheless, the distinction from the former is possible because in the Alceini tribe the atlas has shorter ventral and dorsal arches, a more caudally located ipoapophysis and a wider vertebral foramen, less compressed dorso-ventrally on the cranial side.

3.1.2. Axis

In the present analysis, no *Cervalces* axis from Mosbach were found for a direct comparison with the *M. giganteus*, but giant deer from Ireland were compared with present-day moose. The same features present in *Alces* could probably be extended to its extinct relative.

The cranio-dorsal edge of the cranial shovel (Fig. 2(1)), in lateral view, is oblique and gently curved in the moose, while it is cranially more vertical and then bent to do an horizontal edge in the giant deer. In cranial view, this results in a half circle in the moose and a “U” in the giant deer.

The dorsal edge of the neural spine (Fig. 2(2)), in lateral view, is very convex in the giant deer, while in the moose it is more straight, longer and forward sloping.

Both the cranial and caudal ends of the neural spine (respectively, 3 and 4 in Fig. 2), in lateral view, are more pointed and more elongated (respectively, 3 forward and 4 backward) with a long and straight ventral edge in the moose, while, in the giant deer, the ventral edge is shorter and bends to connect to the dorsal edges of the spine in a more rounded outline.

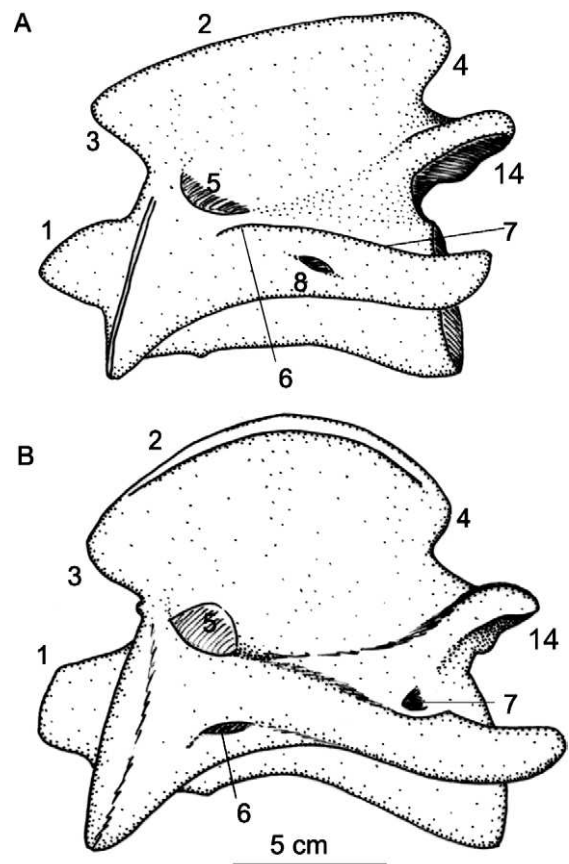


Fig. 2. Axis, lateral view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 2. Axis, vue latérale.

The lateral foramen (Fig. 2(5)), on the cranio-dorsal side of the vertebral body, is large and about circular in the giant deer and is connected with another foramen (Fig. 2(6)) opening downward at the base of the transverse processes and hardly visible in lateral view. In the moose the lateral foramen (5) is smaller and medio-laterally flattened, and the lower foramen (6), is much closer and smaller than in the giant deer because opening on the lateral edges of the transverse processes, rather than under them. Sometimes, in *A. alces*, the wall delimiting this foramen (6) can be incomplete (e.g. the male at UMZC) or lacking at all (e.g. the female at the NHML).

The foramen (Fig. 2(7) and Fig. 3(7)), on the caudo-dorsal side of the vertebral body, is small in the giant deer, while it is larger in the moose but visible only in caudal view because covered by the latero-dorsal belt of the transverse process. In the giant deer, this foramen (7) is connected to the already described lower foramen (6), while in the moose it is connected to a different foramen (Fig. 2(8)) located on the lateral side of the transverse processes, caudally to 5. Foramen 6 is lacking in the giant deer.

In *A. alces*, at the bases of the postzygapophysis, there is another additional small foramen (Fig. 3(9)), visible in caudal view only and lacking in *M. giganteus*.

The transverse processes, in *M. giganteus*, are strong and a little compressed on a dorso-ventral plane. In *A. alces*, the

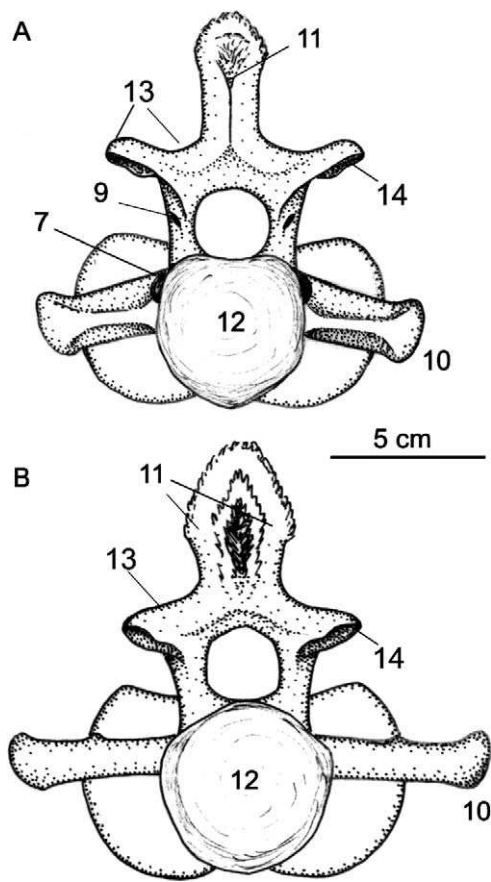


Fig. 3. Axis, caudal view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 3. Axis, vue caudale.

transverse processes are thinner, with sharp medio-caudal edges (Fig. 3(10)), but their latero-cranial edges opens dorsally and ventrally at a right angle to build a vertical belt, flattened in lateral view, that extends caudally beyond the horizontal part. The transverse process has, in this way, a “T” section.

The dorsal edge of the neural spine of *M. giganteus* bifurcates caudally (Fig. 3(11)) and has very rough surfaces, in dorsal and caudal view. In *A. alces* the neural spine is caudally undivided with a medial ridge.

The caudal articular surface of the vertebral body (Fig. 3(12)), in caudal view, is heart-shaped in *A. alces*, with a convex dorsal edge, flat lateral edges and a little pointed ventral edge (the last simply round in the UMZC specimen). In *M. giganteus* this articular surface is about circular.

The dorsal edge of the postzygapophysis (Fig. 3(13)), in caudal view, is longer and concave with the lateral side projecting dorsally in the moose. The same edge, in the giant deer, is shorter and convex.

The articular surface of the postzygapophysis (Fig. 2(14) and Fig. 3(14)) are about flat and oblique in the moose, being all visible in lateral view, while in the giant deer they are concave, with the lateral part horizontally set and no more visible in lateral view.

3.2. Scapula

Scott (1885) states: “The scapula is rather small in proportion to the size of the animal... in shape the bone is more cervine than alcine: the anterior border is straighter and the prescapular fossa smaller than in the moose, while the neck is less contracted and the coracoid larger.” Due to the fragmentary nature of all the *Cervalces* scapulas from Mosbach it was not possible to verify all Scott’s, features except the size of the coracoid that is really larger than in *Alces*.

A fundamental distinction between *Alces/Cervalces* and *M. giganteus* lies in the structure and position of the coracoid with respect to the glenoid cavity. In lateral view, the proximal margin of the coracoid forms together with the outline of the glenoid cavity practically a right angle in the moose and an obtuse angle in the giant deer (Fig. 4(1a)). In proximal view, the coracoid is less protruding from the glenoid cavity outline and a little twisted medially in the moose, while it is more protruding and more symmetrical in the giant deer (Fig. 4(1b)). In some specimen of *A. alces* (i.e. the male of UMZC) the coracoid is less typically Alcine.

The general outline of the glenoid cavity, in proximal view, is more rounded in the moose with a continuous surface, whereas in the giant deer it always possesses a groove (about 15 mm long) which, from the cranial edge, goes toward the middle of the cavity itself (Fig. 4(2)).

The caudal edge of the neck is quite rounded in the giant deer (Fig. 4(3)), while it is sharper in the moose with its lateral outline less or not at all re-entrant with respect to the caudal margin of the glenoid cavity.

3.3. Humerus

The feature described by Pfeiffer (1999a) for the proximal end of the humerus (feature number 1—especially pronounced attachment area of the musculus infraspinatus in *C.*

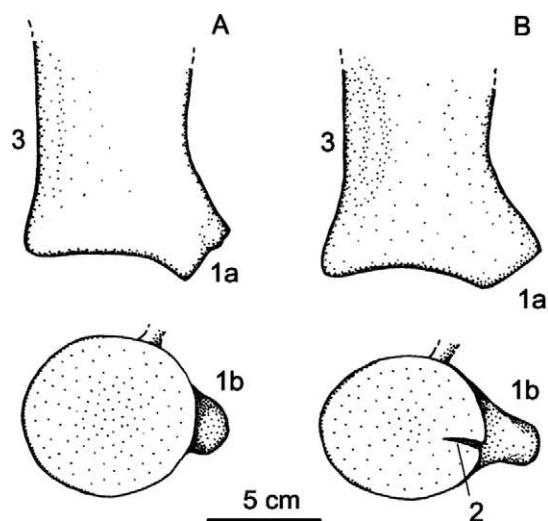


Fig. 4. Scapula, proximal epiphysis. Upper, lateral view; lower, proximal view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 4. Omoplate, épiphyse proximale. Au-dessus vue latérale ; au-dessous vue proximale.

latifrons) is not confirmed here, depending on an erroneous identification of some specimens (Pfeiffer attributed to *C. latifrons* some Bovid specimens in the NHMM collection, e.g. 1987/553, 1969/23 and 1997/692).

In the proximal diaphysis of the humerus, the deltoid tuberosity is well developed and palmarly curved in *M. giganteus*, hardly visible in the *Cervalces* specimens from Mosbach or in the young Norwegian *A. alces*, but pronounced in the UniSI and UMZC *A. alces*. This feature, as all the other muscular insertion surfaces, depends, at least partially, on the sex and the age of the animal and its discriminant value is, in this way, restricted.

The distal epiphysis presents many features useful in identification that, luckily, preserve easily. The four features (2–5) described by Pfeiffer (1999a) are all, at least partially, valid and others can be added.

The radial fossa (or coronoid fossa), on the dorsal side of the distal epiphysis (Fig. 5(2)), in *M. giganteus* is divided into two pits (medial and lateral, respectively) by a small bone bridge. In *Alces* and *Cervalces* the radial fossa lacks this bone bridge and so consists of a single long cavity, or a medial cavity and a rough lateral surface.

The keel on the trochlea humeri (Fig. 5(3) and Fig. 6(3)), running on the articular groove on the proximal radius epiphysis, is more rounded in moose and sharper in *M. giganteus*. This feature is visible only in not abraded trochleae.

In the olecranon fossa, on the palmar side of the distal epiphysis (Fig. 6(4)), the proximal edge of the trochlea humeri is horizontally directed in *Alces* and *Cervalces*, while it rises from the lateral to the medial end in *M. giganteus*.

The epicondylus medialis (or epitrochlea), in palmar view (Fig. 6(5a)), in the moose does not extend distally to the trochlea, while in the giant deer it extends distally well beyond the trochlea and bends medially (Fig. 6(5b)).

The epicondylus lateralis, in palmar view (Fig. 6(6)), is more distally extended in the giant deer than in the moose. In both the animals it hardly extends beyond the latero-proximal

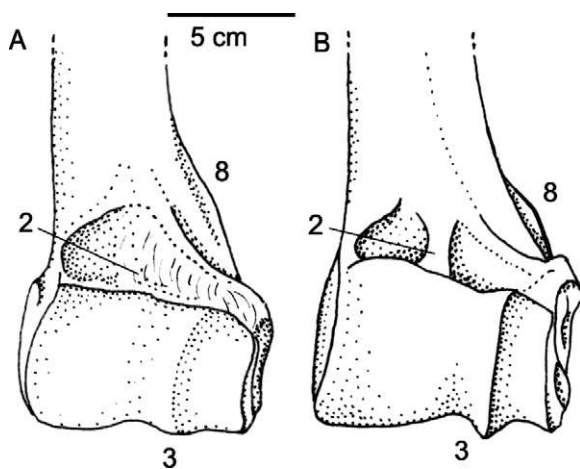


Fig. 5. Humerus, distal epiphysis, dorsal view (after Pfeiffer, 1999a, modified). A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 5. Humérus, épiphyse distale, vue dorsale (d'après Pfeiffer, 1999a, modifié).

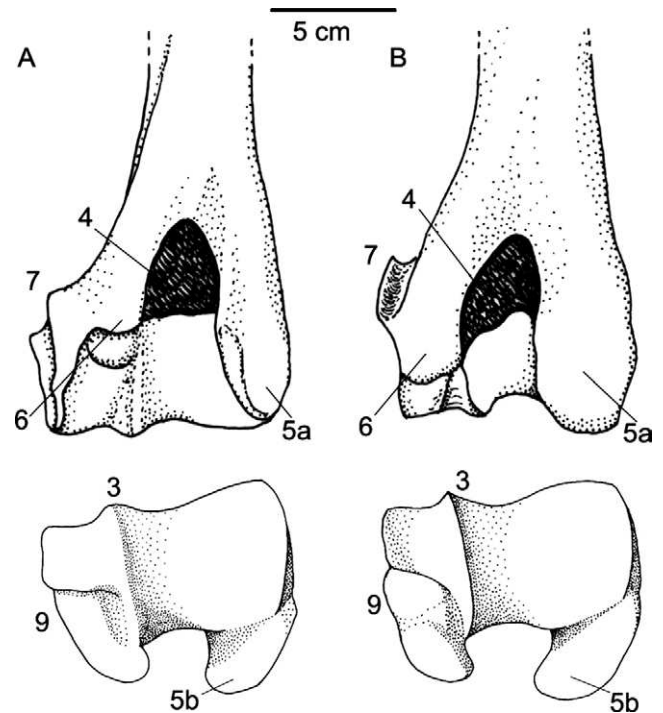


Fig. 6. Humerus, distal epiphysis. Upper, plantar view (after Pfeiffer, 1999a, modified); lower, distal view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 6. Humérus, épiphyse distale. Au-dessus vue plantaire (d'après Pfeiffer, 1999a, modifié) ; au-dessous vue distale.

edge of the trochlea, but this edge is more distally located in *M. giganteus* (see feature number 4).

The lateral edge of the distal epiphysis, in palmar view (Fig. 6(7)), in *M. giganteus* bends abruptly outward and upward, while in *Alces* and *Cervalces* it bends gently outward and does not reach the horizontal plane (Breda, 2002).

The epicondylid crest on the lateral edge of the distal diaphysis, in dorsal view (Fig. 5(8)), in the moose shows a long “pinchment” rising almost to the vertical portion of the diaphysis, while in the giant deer it is pinched only at the distal end (Breda, 2002).

The lateral edge of the distal epiphysis, in distal view (Fig. 6(9)), in *Alces* and *Cervalces*, reaches its more projecting point connected with the palmar edge of the articular surface. In *M. giganteus* the lateral edge of the distal epiphysis protrudes more beyond the articular surface, forming a bulge between the articular surface and the epicondylus lateralis.

3.4. Radius

Pfeiffer (1999a) describes two good features for the proximal epiphysis of the radius (1–2) and two for the diaphysis (3–4). They are here discussed together with the others concerning the proximal epiphysis and those regarding the distal epiphysis.

The groove on the proximal articular facet to the humerus, along which runs the articular keel of the trochlea humeri, has a deep foramen (Fig. 7(1)) in *M. giganteus* sometimes connected with the palmar edge of the groove in contact with

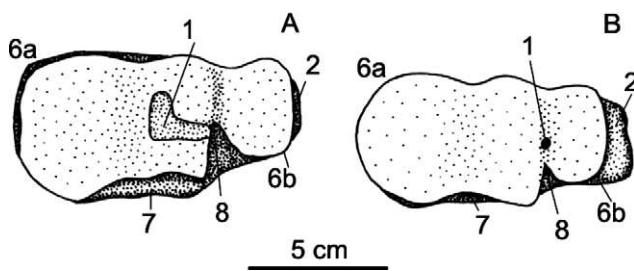


Fig. 7. Radius, proximal epiphysis, proximal view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 7. Radius, épiphyse proximale, vue proximale.

the ulna. In *Alces* and *Cervalces* this foramen is missing and the articular surface can present breaks, flattened and variable in shape.

The general outline of the proximal epiphysis, in proximal view, is more squared in the moose than in the giant deer. This is particularly evident on the medio-dorsal edge (Fig. 7(6a)) and on the latero-palmar edge (Fig. 7(6b)) of the epiphysis, which in *Alces* and *Cervalces* are at angle, while in *M. giganteus* are well-rounded.

The medial articular surface to the ulna (Fig. 7(7)) in the giant deer is substantially vertical, and so it is hardly visible in proximal view. On the contrary, in the moose it has a distal vertical part and then it bends dorsally to reach the articular surface to the humerus, and so is well visible in proximal view. In *A. alces* this articular surface is less laterally developed than in *Cervalces*.

On the palmar edge of the proximal epiphysis, in proximal view, the notch for the lateral articular surfaces of the ulna (Fig. 7(8)), which extends dorsally in the groove along which the articular keel of the trochlea humeri runs, is larger in *Cervalces*. In *M. giganteus* the two edges of the notch are short and almost parallel, while in the moose the medial edge lies parallel to the articular groove for the keel of the humerus and the lateral edge opens. This notch is much deeper in the Mosbach moose than in *A. alces*, reaching about half the length of the groove itself.

Features 7 and 8 reflect the morphology of the articular surfaces of the ulna to radius and humerus.

The dorsal outline of the articular surface of the proximal epiphysis of the radius, in dorsal view (Fig. 8(9)), is markedly undulated in *M. giganteus*, while in *Alces* and *Cervalces* it is gently curved. That is, the edge of the surface, from its more proximally projecting point (scarcely medial to the articular groove), descends gradually toward the medial end in the moose, while it forms an “S” in the giant deer.

The attachment of the ligamentum collaterale laterale (or lateral extensor of phalanges), on the lateral surface of the proximal epiphysis (Fig. 8(2)), is parallel to the lateral diaphysis in *Alces* and *Cervalces* (so, in proximal view, it is hardly visible), while it is laterally directed and more protruding in *M. giganteus* (so, in proximal view, it rises distinctly above the articular surface to the lateral trochlea humeri).

In the moose, the attachment of the ligamentum collaterale mediale (for the bicipital brachial muscle), on the dor-

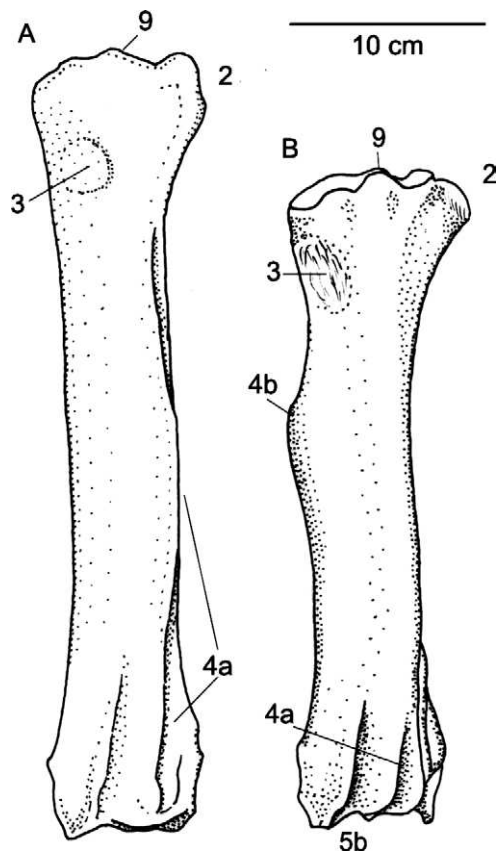


Fig. 8. Radius, dorsal view (after Pfeiffer, 1999a, modified). A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 8. Radius, vue dorsale (d'après Pfeiffer, 1999a, modifié).

sal surface of the proximal diaphysis (Fig. 8(3)), is circular and lies 3–4 cm from the proximal articular surface, while in the giant deer it is more elongated in shape and more proximally located.

The two keels that run parallel to each other from the distal epiphysis, along the dorsal surface of the diaphysis (Fig. 8(4a)), circumscribing the sulcus for the tendon of the metacarpus extensor muscle, are short and sharp in *M. giganteus*, while longer and more rounded in *Alces* and *Cervalces*. In the Alceini, the lateral keel ascends along the diaphysis reaching its proximal portion. In the giant deer males, and to a lesser degree in the females too, the medial side of the diaphysis forms a sharp keel (Fig. 8(4b)) that, in dorsal view, projects medially. This morphology is lacking in the moose (Pfeiffer, 1999a).

On the distal epiphysis, the articular surface to the os carpi radiale has a moderate dorsal concavity (Fig. 9(5)) in the moose. In the giant deer, the same concavity is much more pronounced resulting in that the dorsal edge of the articular surface in dorsal view is concave too (Fig. 8(5b)).

On the distal epiphysis, the crest (Fig. 9(10)) palmarly delimiting the articular surfaces, respectively, to the os carpi intermedium and to the os carpi radiale in *M. giganteus* is vertically set, while in *Alces* (Jacobshagen, 1934) and *Cervalces* it runs obliquely along the epiphysis toward the medial end. This feature is visible in medial view too: in the giant

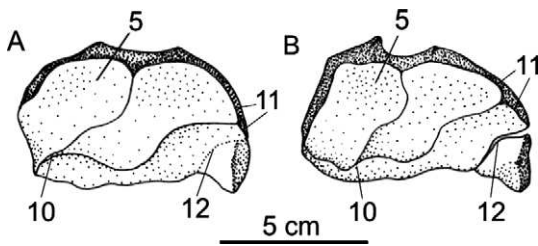


Fig. 9. Radius, distal epiphysis, distal view. **A.** *Alces/Cervalces*. **B.** *M. giganteus*.

Fig. 9. Radius, épiphyse distale, vue distale.

deer, the crest bends toward the bone axis, while in the moose it opens to reach the diaphysis edge at its thickest point (on the growth surface). Probably, the oblique set of this crest permits a smaller flexion of carpal bones in the moose.

The articular surface to the os carpi intermedium is more laterally enlarged in the moose in which it dorsally embraces the articular surface to the os carpi ulnare. In distal view, it results in a different extension of the two surfaces (Fig. 9(11)).

Already Scott (1885) observed that in *Alces* and *Cervalces* the radius and the ulna are fused together for their distal part only, while in most deer the two bones are tightly joined for about 2/3 of their length. Indeed, the fusion between the two diaphyses is more pronounced in *M. giganteus*, so it usually preserves the ulna diaphysis on the radius, while in the moose it is usually lost. On the contrary, in the moose, the healing between distal epiphyses of radius and ulna is very precocious and takes place before the fusion of each epiphysis to the respective diaphysis (Fig. 9(12)).

3.5. Ulna

Sometimes the lateral articular process to the radius (that wedges itself in the notch on the palmar edge of the proximal epiphysis of the radius), on its upper side, bears a small articular surface to the trochlea humeri (Fig. 10(1)). Sher (1974) suggests that this surface is large and triangular in shape in *Cervalces*, while very small or missing in *A. alces*. Both in the *Cervalces* ulnae from Mosbach and in those of the living *A. alces*, the shape and size of this articular surface vary greatly, so it can be considered an individual feature.

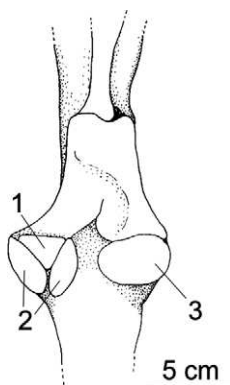


Fig. 10. Ulna of *Alces/Cervalces*, proximal epiphysis, dorsal view.

Fig. 10. Cubitus de *Alces/Cervalces*, épiphyse proximale, vue dorsale.

On the same lateral articular process to the radius, on the two sides of the above-described surface, there are two articular surfaces to the radius (Fig. 10(2)). Sher (1974) suggests that these surfaces are oval in shape and at a right angle in *A. alces*, while in *Cervalces* they are subrectangular and at about a 45° angle. Both in the Mosbach and in the living moose these surfaces are variable in shape and reciprocal angle, but they are larger in the extinct genus. In the giant deer, the lateral articular process to the radius is thinner than in the moose (as reflected in feature 8 of the radius), and the shape of the articular surfaces is variable too.

The medial articular surface to the radius, in dorsal view (Fig. 10(3)), is substantially vertical in *M. giganteus*, while in *Alces* and *Cervalces* its proximal part is obliquely set. This feature (reflecting features 7 of the radius) enables a greater weight unloading on the radius. Sher (1974) suggests that the articular surface is laterally enlarged in *Cervalces* and more medially confined in *A. alces*. In the present analysis this feature proves to be very variable but usually true.

Sher (1974) suggests also that the dorsal outline of the olecranon (Fig. 11(4)), in lateral view, is very concave in *A. alces* and less in *Cervalces*. This outline in the Mosbach *Cervalces* is sometimes also convex, but it is very variable in *A. alces*, so its discriminant value is questioned.

The shape of the top of the olecranon is very variable too. As suggested by Pfeiffer (1999a) the edge of the tuber olecrani forms an angular, flat-topped shape as in all Alceini (because of the great development of the top tuberosity) and a more rounded one in *M. giganteus* (Fig. 11(5)).

3.6. Carpal bones

Heintz (1970) describes some features distinguishing the carpal bones of Cervids and Bovids. The difference lies in the proportions between medial and lateral limb elements: in the Bovids there is a greater reduction in the lateral elements [IV metacarpal, pyramidal (os carpi ulnare) and unciform (os carpal IV)] compared to the medial ones [III metacarpal, scaphoid (os carpi radiale) and capitato-trapezioid (os car-

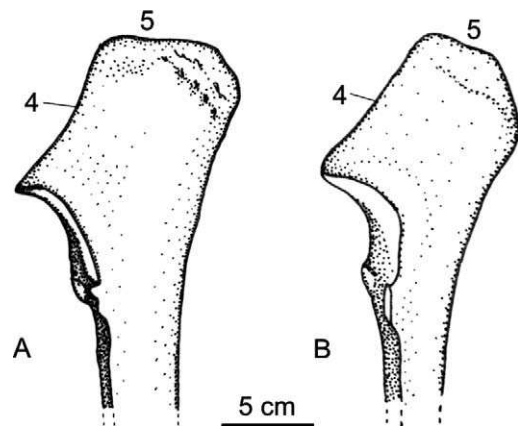


Fig. 11. Ulna, proximal epiphysis and olecranon process, lateral view. **A.** *Alces/Cervalces*. **B.** *M. giganteus*.

Fig. 11. Cubitus, épiphyse proximale et processus olécranien, vue latérale.

pale II et III]). Many *Cervalces* carpal bones are present from Mosbach and their morphology corresponds quite well to that of *A. alces*. *M. giganteus* carpal bones are missing in the NHMM so it was impossible to carry out a direct comparison with *Cervalces* ones. Some *M. giganteus* carpal bones are present in the NHML collection from Ireland and where compared to present-day *A. alces* ones.

The morphology of the proximal elements of the carpal bones has to reflect the morphology of the distal radius. So, in the moose, the proximal articular facet of the scaphoid (os carpi radiale) is less convex because of the corresponding less concave articular surface of the radius (see feature 5 of the radius). In the same way, in the moose, the proximal articular surface of the pyramidal (os carpi ulnare) is less developed because of the corresponding less developed articular surface of the radius (see feature 11 of the radius).

The trapezium (os carpale I), the most medial element of the distal carpus, is reduced to a small vestigial bone, that is free in the telemetacarpal deer and fused to the capitato-trapezoid in the plesimetacarpal deer (Heintz, 1970). This bone is actually present in *A. alces* but, being so small, it is hard to find as a fossil. It is surprisingly preserved, both in right and left fore limb, in the *C. scotti* from New Jersey (Scott, 1885).

In the NHML collection there are three unciforms (os carpale IV) of *M. giganteus* from Ireland. All of them are much more dorso-palmarly elongated than the corresponding elements of the moose, due both to the longer extension of the articular surface and to the presence of a more developed bulge on the distal half of the plantar surface. This bulge, in the moose, is less developed and more medially located.

In the NHML collection there are three capitato-trapezoides (os carpale II and III) of *M. giganteus* from Ireland. In all of them, the distal articular surface to the metacarpus III has a pronounced concavity on its medial side, which results in a concave outline in medial view. This concavity, barely present in the moose, reflects the convexity of the corresponding articular surface of the metacarpus (see feature 1 of the metacarpus).

3.7. Metacarpal bones (III + IV)

Feature 1 by Pfeiffer (1999a) for the proximal epiphysis of the metacarpus states that, in palmar view, the articular facets of the metacarpus III and IV project approximately equally in the moose, while the metacarpus III projects clearly beyond the metacarpus IV in the giant deer. In the present analysis a wide variability was found in the relative heights of the articular facets, but in *M. giganteus* the medial side of the articular facet of the metatarsus III has always a convex portion that, in palmar view, results in a major proximal extension (Fig. 12(1)).

Feature 2 by Pfeiffer maintains that in the moose “both the metacarpus III and IV have a distinctive pit in the middle of their posterior surface that makes contact with the cranial facets”, while “pits are missing in *M. giganteus* that, on the con-

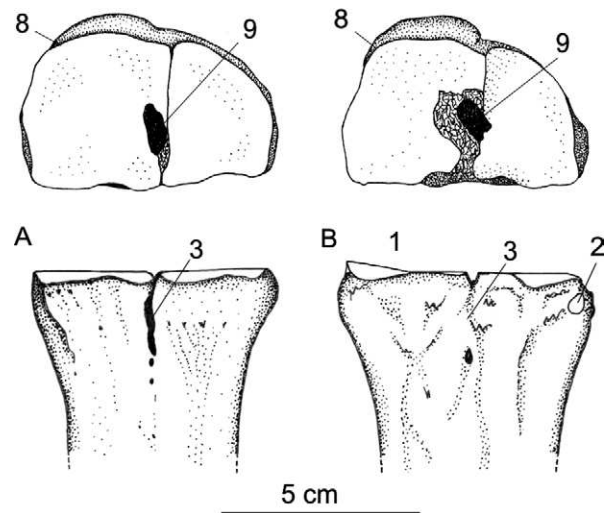


Fig. 12. Metacarpus, proximal epiphysis. Upper, proximal view; lower, plantar view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 12. Métacarpe, épiphyse proximale. Au-dessus vue proximale ; au-dessous vue plantaire.

trary, should have “elevated structures with laterally flattened areas where metacarpals II and V attach”. In the present analysis pits were seen in some *Cervalces* from Mosbach (usually only on one side) and never in other *Cervalces* or in *A. alces*. The elevated structures are present in some moose specimen and can be missing in *M. giganteus* since their development is age dependant. As far as regards the articular facets to metacarpals, they cannot be present in the Alceini that are telemetacarpal deer, but their development is very variable in *M. giganteus*: the one to metacarpal V (Fig. 12(2)) is almost always present (14 specimen on 16 from Ireland) but that to metacarpal II is very rare (two specimens on 16 from Ireland).

Feature number 3 described by Pfeiffer (1999a) retains a limited value. This last concerns the palmar side of the proximal epiphysis that, in the moose, should have a deep groove, running from the proximal articular surface to the proximal interosseus canal, dividing the two metacarpals from each other (Fig. 12(3)). In *M. giganteus*, on the contrary, this groove should be lacking. In the present analysis this feature was found not to be always true, so, it can only be assumed that in the moose the fusion takes place later during ontogenetic development.

The dorsal outline of the proximal epiphysis, in proximal view, is more rounded in *Alces/Cervalces* while in *M. giganteus* it is more squared, particularly evident in the medio-dorsal edge (Fig. 12(8)) that is angular.

The synovial hollow (Fig. 12(9)) between the proximal articular surfaces to the os carpale IV and to the os carpale II + III is small and dorso-palmarly elongated in the moose, while it is larger and isodiametric in the giant deer. Besides, often in the latter there is a main pit, enclosed in a porous area, of unfixed outline, breaking the articular surface.

Pfeiffer’s (1999a) feature 4 for the distal epiphysis is only partially true as it depends on the more developed fusion of metacarpals III and IV in the giant deer and so varies during

individual growth. The dorsal longitudinal groove (Fig. 13(4)) in dorsal view, is usually deeper and ends in a deeper distal interosseus canal in the moose, while it is usually shallow and ends a little more proximally than the small distal interosseus canal in the giant deer.

The gap between the distal trochleae of metacarpals III and IV (feature 5 by Pfeiffer, 1999a) in the moose is proximally enlarged showing a “keyhole” shape, while in the giant deer the two edges are parallel (Fig. 13(5)).

Some features described by Pfeiffer (1999a) for the distal epiphysis of the metacarpus (Pfeiffer’s number 6) and of the metatarsus (Pfeiffer’s numbers 6, 8, 9) have been checked here in both the metapodials, as they consist of structures present in both the fore and hind leg. But none of these features is here confirmed. Number 6 is substituted as follows:

The outline of the proximo-dorsal edge of the articular surfaces of the distal trochleae (Fig. 13(6a)) in dorsal view, is more squared in *M. giganteus* and more rounded, especially on the peripheral side of each toe, in *Alces* and *Cervalces*. Moreover, the dorsal surface of the diaphysis, above the trochleae, is slightly concave in *M. giganteus* and flat or convex in *Alces* and *Cervalces* (Fig. 13(6b)).

The outline of the proximo-plantar edge of the articular surfaces of the distal trochleae (Fig. 30(7)), in plantar view, in *Alces* and *Cervalces* usually possesses some loops breaking the articular surface between the medial keel and the axial and, mostly, the peripheral side of the trochlea. In *M. giganteus* the edge of the trochlea is more regular, sometimes having the articular surface that extends a little proximally on the keel, but never having loops.

Scott (1885) records that the *C. scotti* from New Jersey had very long metacarpal bones and Heintz (1970) records that in the *C. gallicus* holotype the metacarpals are proportionally longer than in *A. alces*. This observation is very interesting but it is based on two specimens only and cannot be verified in *C. carnutorum* and *C. latifrons* because complete fore-legs of these species are lacking.

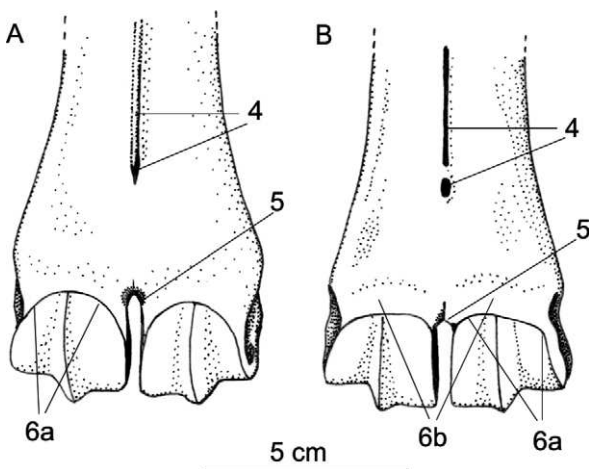


Fig. 13. Metacarpus, distal epiphysis, dorsal view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 13. Métacarpe, épiphyse distale, vue dorsale.

3.8. Telemetacarpal bones (II and V digits)

As already written by Scott (1885), the rudimental metacarpals (II and V) of *C. scotti* have the same shape as those of *A. alces*, but they are longer (Pfeiffer’s assertion, 1999b, that they are complete is erroneous), arriving a little above half of the diaphysis. The telemetacarpals of the *C. gallicus* holotype (Fig. 14) have strong diaphysis but they are fragmentary, so nothing can be stated about their length (Breda, 2001). The telemetacarpals of the *Cervalces* individuals from Grube Cordel, Untermassfeld and Forest Bed, are dimensionally at the upper range of living moose (Breda, 2001).

The strength and length of the II and V metacarpals are ancestral features and so could be present in *Cervalces* which, morphologically, should be closer to the tribe ancestor than *Alces*. But the II and V metacarpal size is too variable at individual level to draw a general conclusion from so few samples. In fact, all the vestigial organs, subjected to low selective pressure, are very variable, as, for example, the plesiometacarpal bones of the fallow deer (Lister and Chapman, 1988).

3.9. Pelvis

All the *M. giganteus* from both Rhine Valley and Ireland (excluding an Irish female in the exhibitions of the NHML) possess a developed ilium-pubis eminence (Fig. 15(1)) forming a muscular insertion process on the pubis ventral edge, close to the acetabulum, while the seven *A. alces* pelvises used here for comparison, the pelvises from Mosbach and the *C. scotti* from New Jersey have a simple tuberosity instead of the ilium-pubis eminence. The development of this tuberosity is even different in the various moose specimen, probably depending on the stage of ontogenetic growth.

M. giganteus possess a large notch (Fig. 15(2)) on the obturator foramen, connected with the acetabular incision, while *A. alces* lack the notch or have it less developed. None of the Mosbach specimen preserves the obturator foramen edge to verify the presence/absence of the notch, but it is present in the *C. scotti* from New Jersey. As for the ilium-pubis eminence, this feature too has not an absolute value because, concerning a surfaces of muscular insertion, it depends on the



Fig. 14. Telemetacarpals of the *C. gallicus* holotype from Sènèze (Haute Loire, France), kept in the University Claude Bernard Lyon-1 as 210542, lateral view.

Fig. 14. Télémétacarpes du type de *C. gallicus* de Sènèze (Haute-Loire, France) conservé à l’Université Claude Bernard Lyon-1 (FSL 210542), vue latérale.

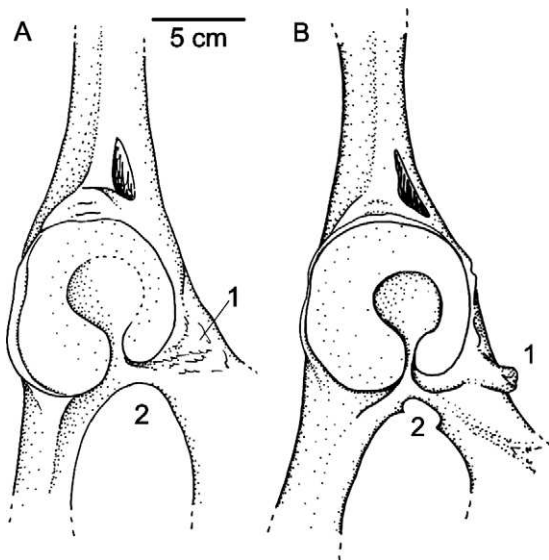


Fig. 15. Pelvis, acetabular portion, lateral view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 15. Pelvis, portion acétabulaire, vue latérale.

age and, probably, the sex of the animal. The absence of the notch testifies the moose, but its presence is not a discriminant value.

3.10. Femur

The features described by Pfeiffer (1999a) for the distal end of the femur (features 1–3) are not confirmed here and are substituted by the followings 1 and 2 in the proximal end and 3 in the distal end of the bone:

Scott (1885), describing the *C. scotti* femur, states: “The great trochanter is higher than in the *Megaceros*, and rises more vertically from the shaft”. The only complete proximal epiphysis from Mosbach confirms this assertion, with a very long trochanter forming an approximate right angle with the femur head. The same angle is right or a little more closed in *A. alces* and larger than 90° in *M. giganteus* (Fig. 16(1)).

Heintz (1970) describes two alternative morphologies, of the proximal and distal epiphysis, respectively, always present together: a cylindrical articular head with an asymmetrical distal trochlea and a spherical articular head with a symmetrical trochlea. The former pair, useful in swift locomotion over flat ground, should be present in all the Villafranchian deer but for *Libralces*, while the latter, useful for crossing uneven ground, should be present in the Ovi-rupi-caprinae and in *Libralces* (Heintz, 1970). The French author, as “*Libralces*”, is considering the *C. gallicus* holotype from Sènèze, but the same morphologies are here confirmed both in *A. alces* and in the *Cervalces* from Mosbach (Fig. 16(2, 3)). Symmetrical trochlea means that there is little size difference between the two trochlea lips, both having sharp edges, while asymmetrical trochlea means that the medial lip is much more developed and swollen than the lateral one and the groove is, consequently, inclined in relation to the bone axis.

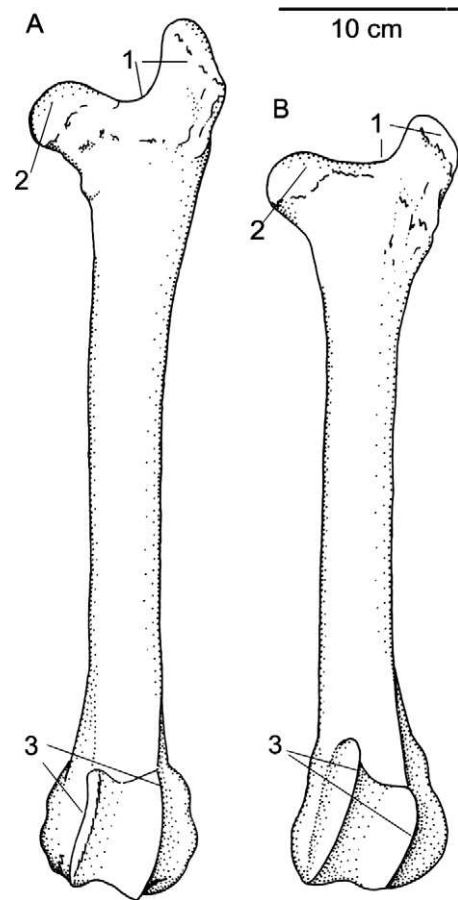


Fig. 16. Femur, dorsal view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 16. Fémur, vue dorsale.

3.11. Tibia

As suggested by Pfeiffer (1999a, feature number 1), the medial and lateral tubercles of the intercondyloid eminence (Fig. 17(1)) in plantar view, project approximately equally in *Alces* and *Cervalces*, while in *M. giganteus* the medial projects beyond the lateral.

Pfeiffer (1999a) describes other features (2–4) for the proximal epiphysis, which are not confirmed here and are substituted as follows:

The tibial crest (Fig. 17(2)) develops more regularly in *M. giganteus*, while in *Alces* and *Cervalces* it exits more abruptly from the diaphysis and bends more laterally. This morphology is very clear both in dorsal and in lateral view.

The plantar-medial edge of the lateral proximal condylus (Fig. 17(3)) in proximal view, is almost straight with the plantar end more laterally located in the moose, while it is curved with the plantar end more medially located in the giant deer. That means that the plantar edge of the lateral condylus is more triangular in shape in the moose and more lobate in the giant deer.

The dorsal edge of the lateral proximal condylus (Fig. 17(4)) in proximal view, bends sharply resulting in an angle in the moose, while in the giant deer it is more rounded. Moreover the angle between this edge and the spina tibialis,

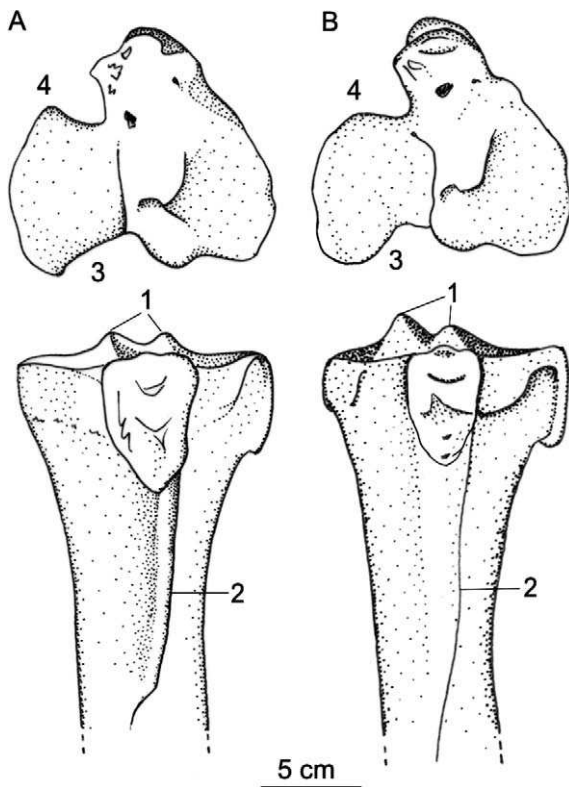


Fig. 17. Tibia, proximal epiphysis. Upper, proximal view; lower, dorsal view. A. *Alces/Cervalces*. B. *M. giganteus*.
 Fig. 17. Tibia, épiphyse proximale. Au-dessus vue proximale ; au-dessous vue dorsale.

in proximal view, is more acute in the moose and more open in the giant deer.

The shape of the ridges on the plantar surface of the proximal diaphysis described by Pfeiffer (1999a, feature number 5) are seen to be variable in both the giant deer and the Alceini tribe, so feature number 5 is substituted as follows:

The articular surface of the chœlea tibiae, in distal view, is divided in a medial and a lateral articular facet that are nearly in contact in *A. alces* (Fig. 18(5) and Fig. 19(5)) and more distant one to the other in *M. giganteus*. In *Cervalces* both the situations were observed.

On the dorsal edge of the main articular surface to the astragalus, in distal view, in *M. giganteus* there is a small but evident articular surface (Fig. 18(6)). This facet is usually absent in the moose or, if present, it is badly defined. The development of this facet, in dorsal view, is sometimes visible as a pronounced point in the lateral edge of the cochlea tibiae (feature 6 by Pfeiffer, 1999a) but it does not have a discriminant value because often present also in the moose (e.g. *Cervalces* from Mosbach NHMM 1962/784, 1964/412, 1968/251) and lacking in *M. giganteus* (e.g. specimen from Upper Rhine Valley, NHMM 1997/725, 1997/724, 1988/115, 1976/90, 1972/11).

Pfeiffer (1999a) describes two features (7 and 8) of the distal epiphysis but their discriminant value is restricted since, involving muscular insertion surfaces, their development is variable:

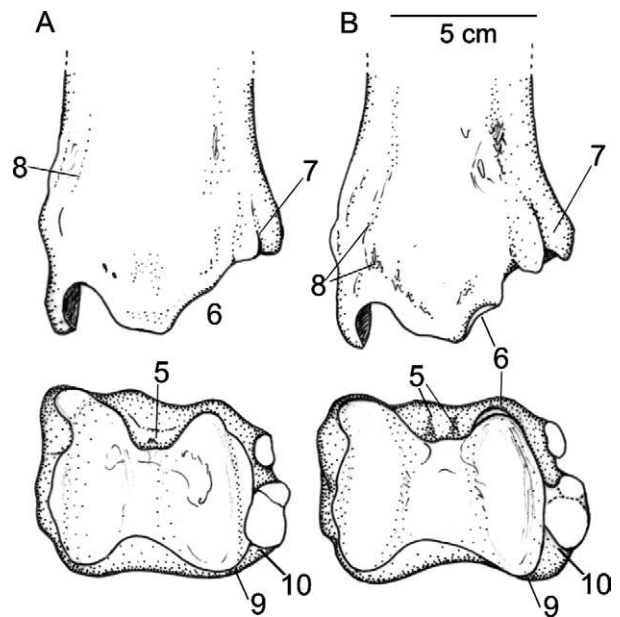


Fig. 18. Tibia, distal epiphysis. Upper, dorsal view; lower, distal view. A. *Alces/Cervalces*. B. *M. giganteus*.
 Fig. 18. Tibia, épiphyse proximale. Au-dessus vue dorsale ; au-dessous vue distale.

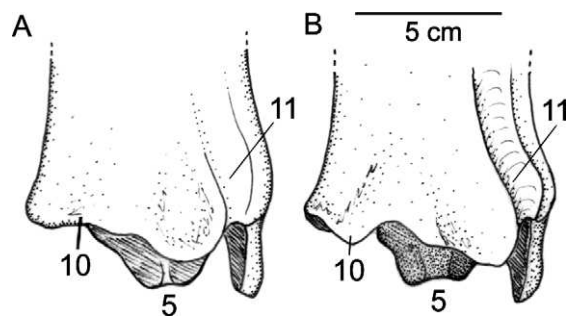


Fig. 19. Tibia, distal epiphysis, plantar view. A. *Alces/Cervalces*. B. *M. giganteus*.
 Fig. 19. Tibia, épiphyse distale, vue plantaire.

M. giganteus should have a distal epiphysis more laterally widened with respect to the diaphysis and a dorsal surface covered by longitudinal ridges (Fig. 18(7)), while the moose should lack these ridges. The morphology of the giant deer well corresponds to the description by Pfeiffer, but many tibiae of *Cervalces* (e.g. NHMM 1962/1330b, 1962/784, 1964/412, 1961/514) show the same lateral widening of the epiphysis and superficial structures.

On the dorso-medial side of the diaphysis, in *M. giganteus* there is a pronounced bulge (indicated by Pfeiffer as the fused malleolus medialis) that rises from the medial side of the diaphysis. This bulge should not be pronounced in the Alceini (Fig. 18(8)), but it actually is in some *Cervalces* specimens (e.g. NHMM 1962/1330b, 1962/784, 1964/412, 1968/251) and *A. alces* (e.g. in the three specimen at the NHML).

The latero-plantar edge of the main articular surface to the astragalus (Fig. 18(9)), in distal view, is more rounded in the moose (the lateral and plantar edges joint about at a right

angle), than in the giant deer (the edges joint at a more acute angle).

The latero-plantar edge of the distal epiphysis is well distally elongated in the giant deer, in which it rises as a wedge between the main articular surface to the astragalus and the plantar side of the articular surface to the malleolus (Fig. 18(10) and Fig. 19(10)).

The sulcus on the latero-plantar side of the diaphysis (Fig. 19(11)), in plantar view, is rounded, demarcated by weak ridges and short in *Alces* and *Cervalces*, while it is longer and well demarcated by sharp ridges in *M. giganteus*.

3.12. Tarsal bones

Scott (1885) records a very developed tarsal ossification in the *C. scotti* from New Jersey with both the small cuneiforms (os tarsale I) joined to the metatarsals and the right large cuneiform (os tarsale II + III) joined to the respective navico-cuboid (os tarsi centrale + os tarsale IV). A developed fusion in the tarsal elements is present in *A. alces* too, first noted by Pavlow (1906) for a fossil specimen from the Moscow neighbors (the three cuneiforms joined to the navico-cuboid) and then by Azzaroli (1952) for two present-day *A. alces* (with the small cuneiform joined to the navico-cuboid and to the large cuneiform, respectively). This occurs even in the *A. alces* at the NHMM, in that at the UMZC and in four of the eleven navico-cuboids from Starr Carr, kept at the NHML. It is a fluctuating feature present in the *C. gallicus* holotype from S n ze (Breda, 2001) where the left large cuneiform is joined to the navico-cuboid (Fig. 20) and also in some *C. latifrons* specimens (NHMM 1963/708 from Mosbach and NHML M.6526 from Overstrand-English Forest Bed). The fusion is in progress in a *C. latifrons* specimen from Voigtstedt, where the large cuneiform (IQW 1966/4620) and the navico-cuboid (IQW 1965/3840) show a dorsal bony process which join them. This extreme fusion was never recorded in *M. giganteus*.

The extreme tarsal fusion, found only in some ruminants from the Mediterranean Islands (Leinders and Sondaar, 1974), results in giving the tarsal joint more strength in lateral movements and so reduces the ability to zigzag across obstacles. It can be linked to the particular locomotion of the moose,

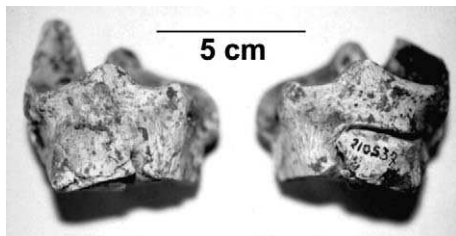


Fig. 20. Tarsal bones of the *C. gallicus* holotype from S n ze (Haute Loire, France), kept in the University Claude Bernard Lyon-1 as 210537, dorsal view. Right, normal situation of Ruminantia; left, abnormal fusion.

Fig. 20. Os tarsiens du type de *C. gallicus* de S n ze (Haute-Loire, France) conserv   l'Universit  Claude Bernard Lyon-1 (FSL 210537), vue dorsale.   droite normale condition des Ruminantia ;   gauche fusion anormale.

termed "stilt" by Flerow (1952), consisting in trotting over low obstacles with a great lift of the metapodials with no suspended phase and, consequently, with low expenditure of energy (Geist, 1999).

Regarding each single large tarsal element, the NHMM lacks an adequate *M. giganteus* collection, so a direct comparison with the respective *Cervalces* tarsal elements was not possible. However, a direct comparison was carried between the numerous giant deer from Ireland kept in the NHML, the present-day moose and the only three *C. latifrons* tarsal element from Forest Bed (Norfolk Coast), present at the NHML (respectively: a calcaneus from East Runton, M6585, an astragalus from Overstrand M17587 and a navico-cuboid from Overstrand M6526). The features found were later verified, by photographic comparison, in the German material of *Cervalces*. The NHML collection of *M. giganteus* from Ireland comprises three mounted skeletons and many isolated elements (11 calcanei, 11 astragali, five navico-cuboids and two large cuneiforms).

3.12.1. Calcaneus

As for all long bones, the shaft of calcaneus is narrower (more medio-laterally compressed) in the moose than in the giant deer. This is well evident also in the distal tuberosity at the end of the shaft that, in distal view, is compressed in the moose (roughly triangular outline with vertex dorsally placed) and as large as long in the giant deer (roughly squared outline).

The sustentaculum is less dorso-plantarly elongated in the moose, with its plantar edge rounded and more developed on its lateral side (close to the shaft), in medial view (Fig. 21(1)), and sloping from lateral to medial side, in plantar view. On the contrary in *M. giganteus* this edge is much more sharp and with a tip on its medial side (Fig. 22(1)), so, in plantar view, it is sloping from medial to lateral side.

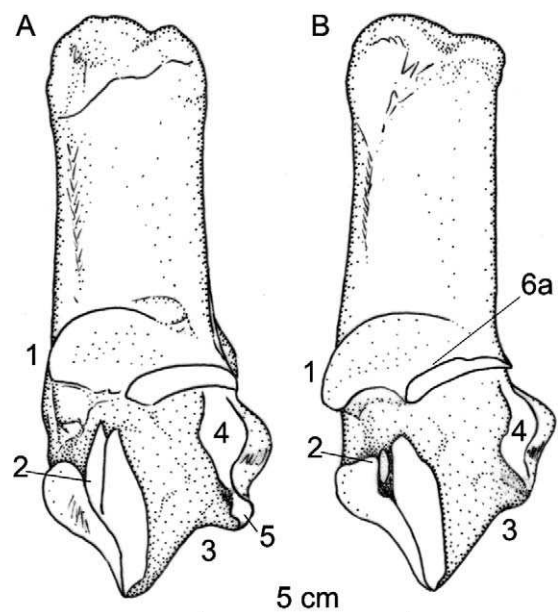


Fig. 21. Calcaneus, medial view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 21. Calcane m, vue m diale.

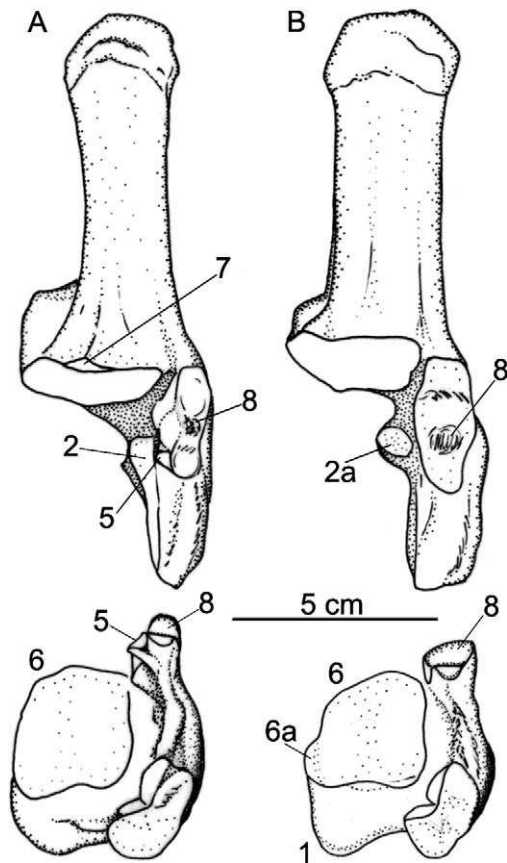


Fig. 22. Calcaneus. Upper, dorsal view; lower, proximal view. A. *Alces/Cervalces*. B. *M. giganteus*.
 Fig. 22. Calcanéum. Au-dessus vue dorsale ; au-dessous vue proximale.

The plantar articular surface to the lateral side of the astragalus in the moose bends medially, on its proximal end, to articulate to the plantar side of the astragalus (Fig. 21(2)). In the giant deer, the facet extends in the sagittal plane only, and an articular surface to the plantar side of the astragalus is lacking or, sometimes, is a separate round facet (Fig. 22(2a)).

The dorsal edge of the calcaneus, between the tip and the articular surfaces to the malleolus (Fig. 21(3)), in lateral view, is concave in *Alces* and *Cervalces* and about straight in *M. giganteus*.

The dorsal articular surface to the lateral side of the astragalus (Fig. 21(4)), which borders the articular facet to the malleolus, in medial view, is more developed in the moose. On the distal end of this articular surface, in the moose there is another small articular surface, obliquely set and medially extending (Fig. 21(5) and Fig. 22(5)). This small facet articulates to a corresponding facet on the astragalus (see feature number 8 of the astragalus). This facet can be more or less developed (it is extremely developed in the *A. alces* of the UMZC) but always present in the moose while it is lacking in *M. giganteus*.

The dorsal edge of the main articular surface of the sustentaculum (Fig. 22(6)), in proximal view, is more straight in the moose and more rounded in the giant deer, which possesses also a medial extension (Fig. 21(6a) and Fig. 22(6a)).

On the dorsal side of the diaphysis, bordering the main articular surface to the astragalus, in dorsal view, *Alces* and *Cervalces* have a small articular surface medio-laterally elongated (Fig. 22(7)). This surface is usually missing in *M. giganteus* or, if present, very badly defined.

The articular surface to the malleolus, in dorsal view, is thinner in the moose (Fig. 22(8)) and, sometimes, a ridge separates it from the articular surface to the lateral side of the astragalus. At the proximal end of this ridge, in the moose, there is the additional small articular facet to the astragalus (see above, Fig. 21(5)).

3.12.2. Astragalus

On the plantar surface of the astragalus, in the giant deer there is a large but simple gap (Fig. 23(1)) between the articular surface to the sustentaculum talii and that to the navico-cuboid, with the distal edge of the articular surface to the sustentaculum having a variable but substantially convex outline. In the moose, there is a deep pit between the two articular surfaces. This feature has its corresponding in the structure of the “tenon lateralis” of the navico-cuboid).

The medial edge of the main articular surface to the sustentaculum talii (Fig. 23(2)), in the moose is fairly straight and distant from the medial side of the bone. The giant deer has an additional small surface, reaching the medial side of the bone and separated from the main articular surface by a straight ridge (2a).

M. giganteus has a sharp tip on the proximal end of the latero-plantar surface of the astragalus (Fig. 23(3) and Fig. 25(3)), well visible in plantar view, while the same outline is simply rounded in the moose.

The proximal end of the medial lip of the proximal trochlea, in the moose extends abruptly outward (Fig. 23(4) and Fig. 24(4)), in frontal and plantar view, doing a clear step that lacks in the giant deer.

The distal end of the medial lip of the proximal trochlea (Fig. 24(5)), in dorsal view, extends medially, through a long and straight edge, in the moose, and through a shorter and curved edge, in the giant deer.

The distal outline of the lateral portion of the distal trochlea (Fig. 23(6a) and Fig. 24(6a)), in dorsal and plantar view,

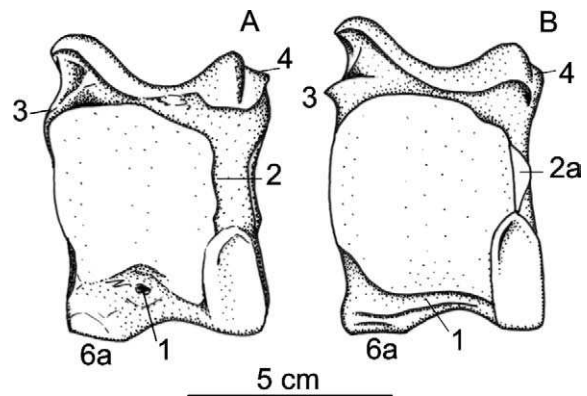


Fig. 23. Astragalus, plantar view. A. *Alces/Cervalces*. B. *M. giganteus*.
 Fig. 23. Astragale, vue plantaire.

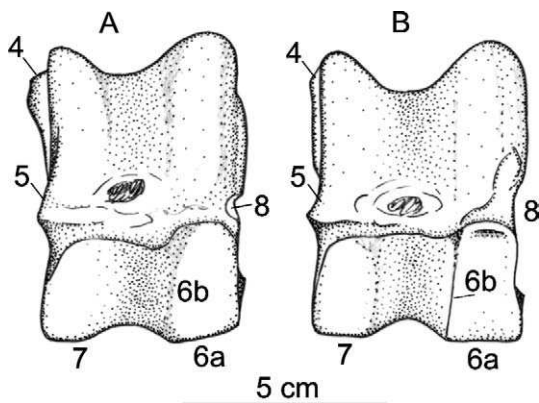


Fig. 24. Astragalus, dorsal view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 24. Astragale, vue dorsale.

is longer, horizontal and straight or little concave in the giant deer, while it is shorter, gently arising laterally and a little convex in the moose. Its medial edge (Fig. 24(6b)) is rather rounded in the moose, and visible as a “line” in *M. giganteus*.

In the same way, the medial portion of the distal trochlea (Fig. 24(7)) is bordered by a rather rounded edge in *M. giganteus*, and by a smooth rounded surface lacking any edge in the moose.

The distal end of the lateral lip of the proximal trochlea (Fig. 24(8) and Fig. 25(8)) joins progressively the dorso-lateral surface of the bone in *M. giganteus*, while in the moose it bends inward forming a very small oblique and distally facing articular surface to the calcaneus (see feature number 5). In the *A. alces* at the UMZC this facet is even horizontal because of the great development and protruding of the corresponding facet of the calcaneus.

The plantar end of the proximo-lateral trochlea (Fig. 25(9)), in lateral view, in the moose is closer to the plantar tip of the trochlea.

M. giganteus has a pronounced depression (pit) on the medial surface of the bone, in correspondence of the axis of the distal articular trochlea, while the moose usually lacks this pit or has it very few pronounced.

3.12.3. Navico-cuboid

The “body” of the bone is more proximo-distally elongated in the moose than in the giant deer, reflecting the gen-

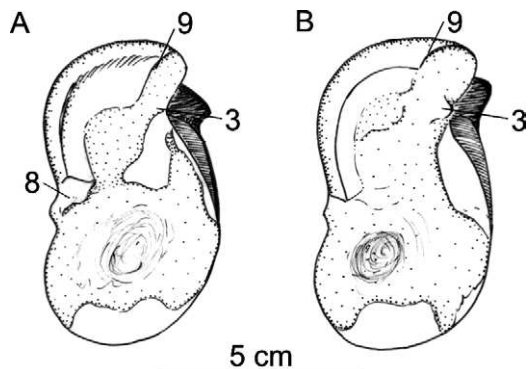


Fig. 25. Astragalus, lateral view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 25. Astragale, vue latérale.

eral shorter limbs of the latter. This is more evident in dorsal view (Fig. 26), looking at the distance between the proximal articular surface to the astragalus and the distal articular surfaces, respectively, to the large cuneiform (medial) and to the metatarsus IV (lateral). This difference in proportions is codified by the rate between the medial or lateral height of the dorsal surface (respectively, Hm and Hl) and the greatest breadth (GB) of the bone, resulting smaller in the giant deer. The means of this rate follow, respectively, in *Cervalces*, in recent *A. alces* and in *M. giganteus* with the sample size (n): Hm/GB (0.318 n = 17; 0.324 n = 8; 0.228 n = 7), Hl/GB (0.404 n = 17; 0.471 n = 8; 0.359 n = 7).

The articular surface of the “tenon lateralis” (lateral tooth) (Fig. 26(1)), in dorsal view, in the giant deer is parted by a marked gap from the main articular surface to the trochlea of the astragalus, while in the moose it is in conjunction on its lateral side. Moreover, in the moose this facet is surrounded by another facet (Fig. 26(2)), which bends around its medial and proximal sides and articulates to the deep pit of the astragalus (see feature 1 of the astragalus). Facet 2 of the navico-cuboid and, consequently, pit 1 of the astragalus are lacking in the giant deer.

On the lateral edge of the articular surface to the large cuneiform, *M. giganteus* has an additional dorso-plantarly elongated small facet, parallel to the sagittal plane (Fig. 27(3)). This facet is lacking in *Alces* and *Cervalces*. The equivalent of this articular surface should be present on the proximal edge of the lateral side of the large cuneiform in the giant deer but not in the moose.

The plantar articular surface to the metatarsal (Fig. 27(4)), in distal view, is thin and more laterally elongated in the moose, while it is shorter and more “rhomboid” in the giant deer. This feature is reflected in the shape of the corresponding articular surface of the metatarsal proximal epiphysis (see feature 2 of the metatarsus).

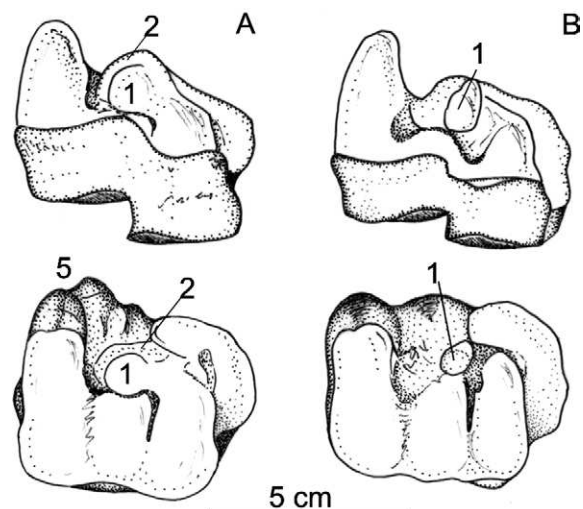


Fig. 26. Navico-cuboid. Upper, dorsal view; lower, proximal view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 26. Cubo-naviculaire. Au-dessus vue dorsale ; au-dessous vue proximale.

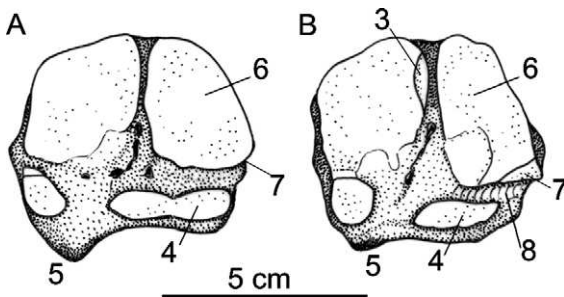


Fig. 27. Navico-cuboid, distal view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 27. Cubo-naviculaire, vue distale.

The plantar surface of the navico-cuboid, in the moose has a well developed bulge (5 in Figs. 26–28), particularly evident in distal view as an extension of the median part of the plantar outline that elongate backward far from the articular facet to the small cuneiform. In *M. giganteus* only a small bulge is present.

The articular surface to the metatarsus IV (Fig. 27(6)), in distal view, is less dorso-plantarly elongated in *Alces* and *Cervalces* than in *M. giganteus*.

The plantar-lateral portion of the articular surface to the metatarsus IV (Fig. 27(7) and Fig. 28(7)), in distal view, is flat or slightly concave in *Alces* and *Cervalces*. On the contrary, in *M. giganteus* it is convex and bends proximally to form a quite separate triangular small surface. This morphology is reflected in the articular surface of the metatarsus (see feature 1 of the metatarsus).

In the giant deer, the articular surfaces to the metatarsus (the plantar one and that to metatarsus IV) are separated by a deep groove (Fig. 27(8) and Fig. 28(8)), well visible in lateral view. This groove is not present in the moose.

The articular surface to the calcaneus (Fig. 28(9)), in lateral view, extends less distally in the moose, its distal end not reaching halfway of the lateral height of the bone, while in the giant deer the distal end of the same facet runs halfway or lower.

3.12.4. Large cuneiform

The NHML has only two isolated large cuneiforms of *M. giganteus*. On both these specimens it was possible to confirm the presence, on the proximo-lateral edge, of a small elongated articular facet, bordering the main articular facet to the navico-cuboid, that articulates on the corresponding

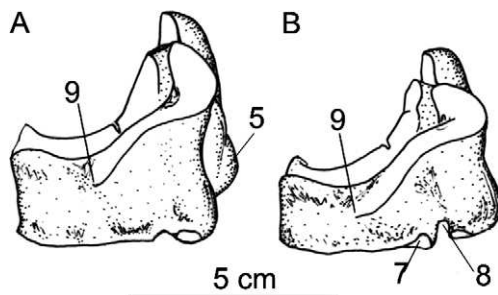


Fig. 28. Navico-cuboid, lateral view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 28. Cubo-naviculaire, vue latérale.

facet on the navico-cuboid above described (see feature 3 of the navico-cuboid). This small facet is absent in living moose, in the *C. gallicus* holotype from Sènèze and in the only *C. latifrons* specimen present in the examined collections (Voigtstedt, IQW 1966/4619, Breda, 2001).

3.13. Metatarsal bones (III + IV)

Feature number 1 described by Pfeiffer (1999a) on the morphology of the proximal articular surfaces of the metatarsals is not confirmed here, since both *Alces* and *Cervalces* show a wide variation in the morphology of this surface. Feature number 1 is substituted here by the following 1:

The proximal articular surface to the navico-cuboid (Fig. 29(1)), in proximal view, has a roughly straight plantar edge in the moose, while in the giant deer the lateral part elongates backwardly and bends proximally to form a quite separate triangular small surface. This particular shape fit with the corresponding facet of the navico-cuboid as above described (number 7).

Pfeiffer's feature number 2 is confirmed only partially, while 3–5 are good features.

The plantar articular surface to the navico-cuboid (Fig. 29(2)), in proximal view, is thinner and more laterally elongated in the moose, while it is shorter and more dorso-plantarly developed in the giant deer. But in both the deer, the plantar outline of this surface forms an axial peak between

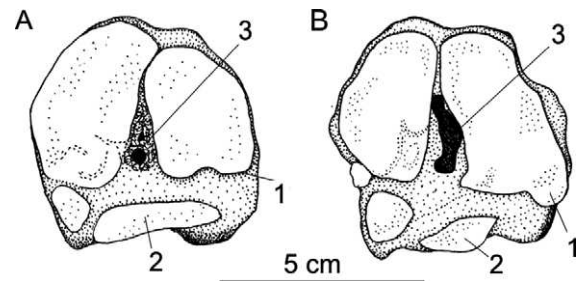


Fig. 29. Metatarsus, proximal epiphysis, proximal view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 29. Métatarse, épiphyse proximale, vue proximale.

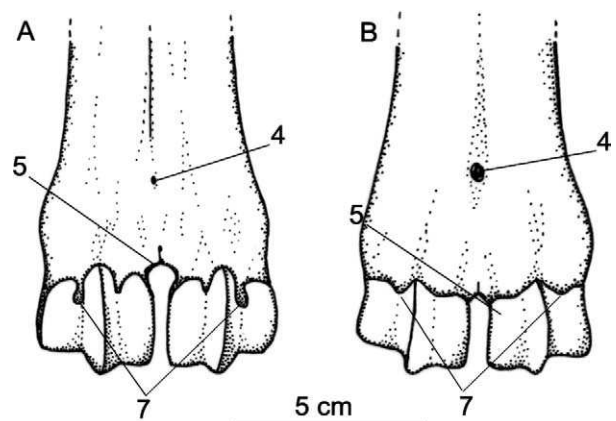


Fig. 30. Metatarsus, distal epiphysis, plantar view. A. *Alces/Cervalces*. B. *M. giganteus*.
Fig. 30. Métatarse, épiphyse distale, vue plantaire.

metatarsal III and IV that is a little more medially located in the moose. Sher (1974) suggests this peak is typical of *Cervalces* aff. *C. latifrons* compared with *A. alces*, but, in the present analysis, no differences were found between the two genera.

The foramen on the proximal articular surface, between metatarsal III and IV (Fig. 29(3)) in proximal view, is large and dorso-plantarly elongated in the giant deer, while it consists in a smaller main pit, enclosed in a porous area, which can vary in shape, in the moose.

The plantar interosseus canal on the distal epiphysis (Fig. 30(4)) in plantar view, is smaller in the moose and larger in the giant deer. It is worthwhile to underline that this canal is always larger in the metacarpals, both of *Alces* and *Cervalces*, than in the respective metatarsal, so this feature is useful in distinguishing the isolated distal epiphysis of the fore and hind metapodials.

As for the metacarpals, the gap between the distal trochleae of metatarsals III and IV (Pfeiffer's feature 5, 1999a) in the moose is proximally enlarged showing a "keyhole" shape, while in the giant deer the two edges are parallel (Fig. 30(5)).

As already stated about metacarpal bones, feature numbers 6, 8, 9 are considered not valid. Feature number 6 is substituted as follows:

As for the metacarpals, the outline of the proximo-dorsal edge of the articular surfaces of the distal trochleae (Fig. 13(6a)), in dorsal view, is more squared in *M. giganteus* and more rounded, especially on the peripheral side of each toe, in *Alces* and *Cervalces*. As for the metacarpals too, the dorsal surface of the diaphysis, above the trochleae, is slightly concave in *M. giganteus* and flat or convex in *Alces* and *Cervalces* (Fig. 13(6b)).

Pfeiffer's feature number 7 (1999a) considers the greater thinning of the distal diaphysis with regard to the epiphysis in the moose, but this thinning is typical of all the long bones of the Alceini (see conclusions) so it would be reductive to consider it as diagnostic for metatarsals. Feature number 7 is substituted as follows:

As for the metacarpals, the outline of the proximo-plantar edge of the articular surfaces of the distal trochleae (Fig. 30(7)), in plantar view, in *Alces* and *Cervalces* usually possesses some loops breaking the articular surface between the medial keel and the axial and, mostly, the peripheral side of the trochlea. In *M. giganteus* the edge of the trochlea is more regular, sometimes having the articular surface that extends a little proximally on the keel, but never having loops.

3.14. Phalanges

When possessing both the anterior and posterior phalanges of the same specimen, it is easy to distinguish them for the greater length of the latter (Scott, 1885; Chaix and Desse, 1981) [Pfeiffer (1999a) is wrong in saying that in the moose the anterior phalanges are longer]. Isolated phalanges are, on the contrary, difficult to assign to the fore or hind leg. How-

ever, all the phalanges (first, second and ungual) are more elongated in the moose than in the giant deer.

Schmidt (1934) maintains that *C. latifrons* had shorter toes than *A. alces*, and Pfeiffer (1999b) agrees suggesting that *Cervalces* was less adapted than living moose to moving over soft grounds (swampy soils in summer and uncrushed snow in winter). This assumption could be verified only by computing the ratio of phalanx length to that of other long bones in the same individual, which is not the case in either the *C. latifrons* from Bilshausen, analyzed by Schmidt (1934), or those from Mosbach and Voigtstedt, considered by Pfeiffer (1999b) (Breda, 2001). In Europe, the only complete *Cervalces* skeleton is the *C. gallicus* holotype from S n ze, in which this ratio is about the same or little higher (depending on the long bone considered) than in living moose (Breda, 2001), suggesting that its phalanges were proportionally at least as long as in living moose. In the *C. scotti* holotype the same ratio is higher than in living moose, confirming what already stated by Scott (1885) for the North American species.

Probably Schmidt (1934) and Pfeiffer (1999b) hypothesized the phalanx length from the stocky proportions without verifying the length ratio of phalanx to other bony elements. The exceptional stoutness of the *C. latifrons* phalanges is obviously justified by its huge body mass, if compared to living moose. If the phalanges had increased isometrically, as occurs for the linear dimensions, they would not be strong enough to bear the body weight, which increases with the volume and so with the cube of the linear dimensions.

The characters, grouped under phalanx number, are valid for both front and rear feet:

3.14.1. First Phalanx

The proximal tuberosities for muscular insertion on the ventral side of the diaphysis (Fig. 31(1); features 1 and 4 in Pfeiffer, 1999a) are more developed in the giant deer than in the moose. In *A. alces* (Chaix and Desse, 1981) and probably in *Cervalces*, the axial tuberosity is more proximo-distally elongated in the anterior phalanges, in which it is visible in axial view too.

The ligament attachment on the distal-ventral side of the diaphysis (Fig. 31(2); features 2 and 5 in Pfeiffer, 1999a) is hardly visible in the moose (a little more evident in the pos-

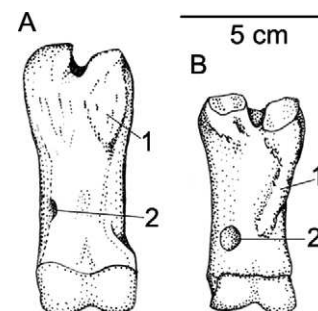


Fig. 31. First phalanx, palmar/plantar view (after Pfeiffer, 1999a, modified). A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 31. Phalange I, vue palmaire/plantaire (d'apr s Pfeiffer, 1999a, modifi ).

terior phalanges), while it is elevated and more distally located in the giant deer.

Both these features by Pfeiffer (1999a), because concerning surfaces for muscular insertion, are depending on the age and the sex of the animal, so their discriminant value is restricted (young giant deer can look more like old and strong moose).

Pfeiffer's feature number three is not confirmed here.

3.14.2. Second phalanx

The distal trochlea is deeper in the moose than in the giant deer, with the dorsal and ventral edges more proximally elongated (well visible in axial and peripheral view).

In the moose, the distal trochlea of the anterior phalanges is more asymmetrical in dorsal view, with the axial side more proximally elongated than the peripheral one (Chaix and Desse, 1981). In axial view, the dorsal edge of the trochlea is lower than the ventral edge in the posterior phalanx, while in the anterior phalanx it is the opposite.

3.14.3. Third phalanx

The axial side of the solea (Fig. 32(1); feature 6 in Pfeiffer, 1999a) in ventral view, is nearly straight and with a distinct edge in the moose, while it is concave and rounded in the giant deer.

The proximal articular surfaces in the moose are typical (Chaix and Desse, 1981): the peripheral surface has a dorsal process that bends medially and ascends on the pyramidal eminence, embracing the axial surface (Fig. 32(2)). This morphology ensures a wide spread of the toes that, together with the length of the phalanx, can be interpreted as an adaptation to prevent sinking on a soft ground (Breda et al., 2005).

Pfeiffer (1999a) suggests also that *M. giganteus* has a third small articular surface (to the small sesamoid; Fig. 32(3)), less expressed in the posterior phalanx, and that this surface should be lacking in *C. latifrons*. On the contrary, Chaix and Desse (1981) record this third articular surface in the posterior phalanx of *A. alces*. As regards personal observations, on the ventral side of the two main articular surfaces (axial and peripheral) of the moose, there is only a tuberosity, more developed in the posterior phalanges but lacking the articular surface.

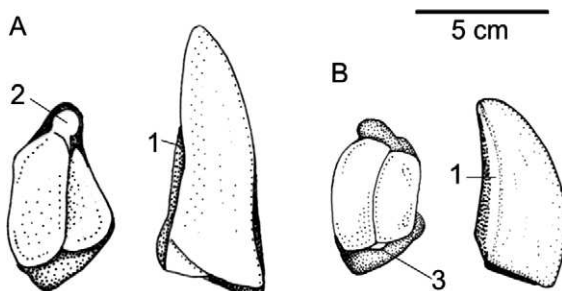


Fig. 32. Third phalanx (after Pfeiffer, 1999a, modified). Left, proximal view; lower, palmar/plantar view. A. *Alces/Cervalces*. B. *M. giganteus*.

Fig. 32. Phalange III (d'après Pfeiffer, 1999a, modifié). À gauche vue proximale ; à droite vue palmaire/plantaire.

3.14.4. Rudimental phalanges

Scott (1885) records that the rudimental phalanges (II and V digit) were stronger in *C. scotti* than in *A. alces* and suggests they were an adaptation to the swampy summer grounds. The only other *Cervalces* rudimental phalanges I could analyze (the *C. gallicus* holotype and the *C. latifrons* specimen from Grube Cordel) are not stronger than in living moose. But two specimens are far too few because these phalanges, as any rudimental organ, can vary greatly in individual size as no longer subjected to natural selection. If *Cervalces* had stronger rudimental phalanges than *Alces*, it should be an archaic feature rather than a secondary adaptation.

4. Discussion and conclusions

On a general level, *M. giganteus*, compared to *Cervalces* and *Alces*, has a stronger postcranial skeleton, not only for the breadth/length rate of each long bone but also for both the ossification level and the development of the muscular insertion surfaces. In this way, moose in advanced age could show morphologies usually more typical of giant deer and, on the contrary, young giant deer could appear more like the moose because of their reduced level of bony sutures and of their reduced development of surface bony structures. This includes some of the identification characters described in this work, so limiting their usefulness and discriminant value; these are atlas 3, proximal humerus, metacarpal 3 and 4, pelvis 1 and 2, tibia 7 and 8, first phalanx 1 and 2. In this respect, moose seem to be substantially more neothernic than giant deer, not reaching, usually, the same level of bony sutures and the same development of tuberosities and crests for muscular insertion.

Moreover, the present analysis demonstrates a substantial uniformity in the postcranial skeleton of the three Eurasian species of the genus *Cervalces*. *A. alces* is differentiated, at a postcranial level, only for the more pronounced thinning of diaphysis with regard to epiphysis, a feature already typical of Alceini tribe within the other Old World deer but for the reindeer. Because the diameter of the diaphysis continues to increase through life as layers of periosteal bone are added, the thinner diaphysis of *A. alces*, together with its smaller size in comparison to *C. latifrons*, can be regarded as a neothernic character. Geist (1999) suggests that this reduction in size could have had an adaptive meaning in a source-limited environment.

As already discovered for the dental morphology (Breda, 2001), in the Alceini tribe the interspecific and intergeneric variability is very low and does not encompass the individual variability in the epiphyseal proportions and in the morphology of the articular surfaces. This confirms what Sher already stated (1987) that the Alceini, in Upper Pliocene, constituted an already well-defined morphological type that did not undergo further postcranial structural remodeling.

Here only one morphology was found, at postcranial level, differentiating the extinct genus from the living one: the stron-

ger proximal connection ulna/radius (both the medial and lateral processes). This feature is probably related to the greater load on the elbow joint because of the wider antlers (in the giant deer the proximal connection ulna/radius was even less developed, but it was counterbalanced by the tighter connection on the medial and distal diaphysis). This, together with other particular features above-described (i.e. femur structure, extreme tarsal fusion, length and wide spreading of the phalanges) and with an almost identical teeth structure (Breda, 2001; Breda et al., 2005) shared by present-day *A. alces* and *Cervalces*, but by no other deer, may suggest that *Cervalces* could be adapted to move on a similar ground and to browse the same kind of food of its living relative. This seems to be confirmed by a detailed palynological analysis of the pollens extracted from a *C. latifrons* specimen from Fornaci di Ranica (Bergamo, Northern Italy) (Breda et al., 2005). The botanical record of the moose bearing level from Ranica, suggests a landscape dominated by open meadow-steppe vegetation with wet pockets of riparian forbs and cold springs, that well corresponds with today moose habitat (Breda et al., 2005).

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