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Phylogeny of the giant deer with palmate brow tines *Megaloceros* from west and *Sinomegaceros* from east Eurasia

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Abstract

Giant deer with palmate brow tines were placed either in a single genus, or those from west Eurasia were placed in *Megaloceros* and those from the east in *Sinomegaceros*, which implies local evolution. In order to see whether dispersals between the two areas may have occurred, we studied the morphology and interpreted the phylogeny of these deer.

The phylogenetic model proposed does not support any dispersals between east and west after the appearance of the first species of each genus, but it does support the recognition of two separate genera.

The ecological significance of some of the morphological characters is interpreted. Thicker molar enamel, reduced posterior molars, larger premolars and a P_4 with a lesser degree of "molarisation" suggests that *Megaloceros savini* adapted to a diet that includes coarser and harder food. Elevated mandibular condyles, thin molar enamel, and P_4 that are predominantly "molarized" suggest that *Megaloceros giganteus* and *Sinomegaceros yabei* shifted towards grazing larger quantities of not very hard food. Very robust metapodials evolved several times in western Eurasian giant deer: during the Early Pleistocene in the *Megaloceros solilhacus* group, not later than the late Middle Pleistocene in *M. giganteus* and it increased in the Late Pleistocene *M. giganteus*. Since the character did not evolve in the east Eurasian giant deer, it might be related to some aspect of the west Eurasian environment, that was not present in east Eurasia.

1. Introduction

Along with mammoths and wooly rhinos, the giant deer, are emblematic for the Pleistocene and have a wide distribution in Europe and northern Asia. There are various species, which some place in a single genus, while others place them in different genera or subgenera. The grouping in different genera or subgenera reflects to some extend a geographical separation, with the west Eurasian species being placed in *Megaloceros* and the east Eurasian species in *Sinomegaceros*. Such a classification suggests that, local evolution was predominant. However, many Pleistocene dispersals of Asian taxa into Europe have been recorded, while dispersals in the opposite direction may have occurred as well. There are various characters that appeared during the Middle and Late Pleistocene in both east and west Eurasian species and the question arises, whether dispersals of *Megaloceros* between these areas may not have been more common than usually assumed. If such dispersals existed, they would present opportunities for biostratigraphic correlations and further study of biogeography in relation to environment or climate. In order to investigate this question, we studied the morphology and biometry and interpreted the phylogeny of the east and west Eurasian giant deer with palmate brow tines.

There is no universally accepted nomenclature of the giant deer and synonyms abound, but opinions diverge on which of them are synonyms and which names to use. It may be helpful for the reader to present a small overview. The term "giant deer" is an informal name that translates the formal name *Megaloceros* Brookes, 1828 (= *Megaceros* Owen, 1844). Azzaroli (1953) included a large number of species in this genus, but recognized two groups, the "*Megaceros verticornis* group" with brow tines with rounded section and the "*Megaceros giganteus* group"

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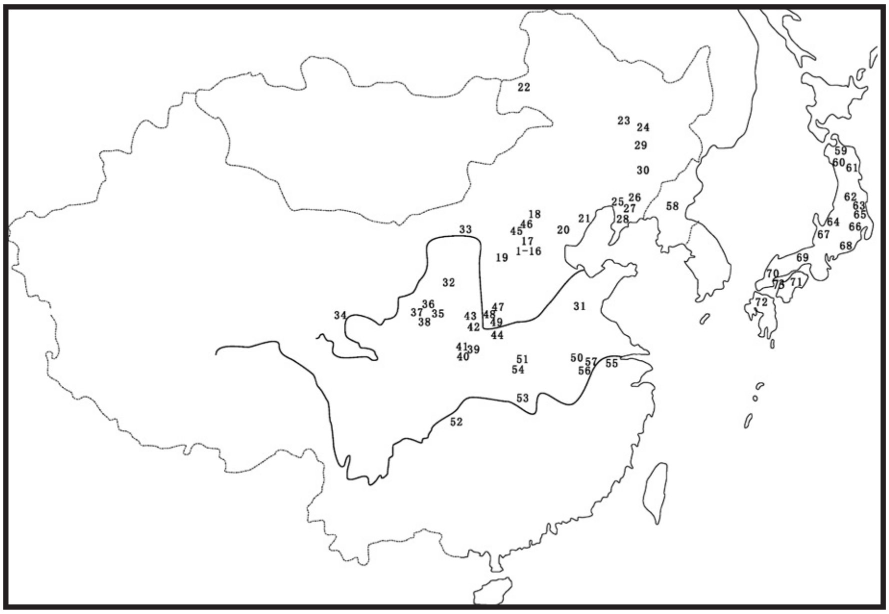
with flattened or palmate brow tines. The former group of species is sometimes placed in *Megaceroides* or *Praemegaceros*. Another large deer is *Eucladoceros*, and material that some assign to *Eucladoceros giulii* (Kahlke, 1997; van der Made, 1999a) is considered by others to represent "gracile *Megaceroides*/*Praemegaceros*". All these forms are included here in the loose term "giant deer", but this does not imply a-priori any close relationship. *Megaloceros giganteus* is believed to be closely related to the living fallow deer *Dama* (Lister et al., 2005) or to *Cervus elaphus* and *Cervus nippon* (Pfeiffer, 1999).

In a review of a paper by Young (1932), that described the giant deer from Zhoukoudian, Dietrich (1933) introduced the subgeneric name *Sinomegaceros*, with type species *Cervus (Sinomegaceros) pachyosteus*. Possibly due to the peculiar context in which the name was introduced, it took some time for the name to become used and the name is not included by Simpson (1945) in his well known classification of the mammals. H.D. Kahlke and Hu (1957) and R.D. Kahlke (1994, 1999) treated *Sinomegaceros* as a subgenus of *Megaloceros*. Shikama and Tsugawa (1962) and Otsuka and Shikama (1977) considered *Sinomegaceros* an independent genus. Vislobokova (1990) and Vislobokova and Hu (1990) recognized three branches of giant deer, that originated in the Late Miocene and Early Pliocene: one including the Pliocene genus *Orchogonoceros* and leading to *Praemegaceros*, another one including the Late Pliocene *Sinomegaceros tadzhikistanis* and giving rise to several other species of the same genus, and a third one originating from the Late Pliocene *Arvernoceros ardei* and leading to *Praedama* and *M. giganteus*. Xue and Zhang (1991) and Huang (1991) did not recognize *Sinomegaceros*



1 Zhoukoudian Loc. 1
2 Zhoukoudian Loc. 2
3 Zhoukoudian Loc. 3
4 Zhoukoudian Loc. 4
5 Zhoukoudian Loc. 7
6 Zhoukoudian Loc. 9
7 Zhoukoudian Loc. 11
8 Zhoukoudian Loc. 13
9 Zhoukoudian Loc. 13A
10 Zhoukoudian Loc. 15
11 Zhoukoudian Loc. 20
12 Zhoukoudian Loc. 21
13 Zhoukoudian Loc. 22
14 Zhoukoudian Loc. 23
15 Zhoukoudian Loc. 24
16 Zhoukoudian West Cave
17 Mentougou
18 Chicheng
19 Jingxing
20 Yutian
21 Qinhuangdao
22 Manzhouli
23 Guxiangtun
24 Yanjiagang
25 Jinniushan
26 Miaohoushan
27 Haicheng
28 Gulongshan
29 Yushu
30 Ji'an
31 Yiyuan
32 Sjara-osso-gol
33 Baotou
34 Gonghe
35 Qingyang
36 Huanxian
37 Zhenyuan
38 Changwu
39 Gongwangling
40 Laochihe
41 Chenjiawo
42 Dali
43 Luochuan
44 Sanmenxia
45 Xujiayao
46 Nihewan
47 Dingcun
48 Houma
49 Ruicheng
50 Huainan
51 Nanzhao
52 Badong
53 Jingmen
54 Yunxian
55 Tangshan
56 Chaoxian
57 Hexian
58 Xiangyuan, North Korea
59-73 Japan
66 Tomioka, Gunma Prefecture
73 Seto Sea

Fig. 1. The geograpic position of the east Asian localities with giant deer with palmate brow tines.

and placed these species in *Megaloceros*. McKenna and Bell (1997) classified *Megaloceros* (including *Praedama*) and *Sinomegaceros* as different genera, within a tribe Megacerini within the Cervinae.

The giant deer with palmate brow tines were wide spread in east Asia (Fig. 1; Table 1). Names proposed for the east and central Asian giant deer with palmate brow tines, include: *S. tadzhikistanis* Vislobokova, 1988, *S. konwanlinensis* Chow, Hu and Lee, 1965, *S. flabellatus* (Teilhard de Chardin, 1936), *S. pachyosteus* (Young, 1932), *S. ordosianus* (Young, 1932), *S. yabei* Shikama, 1938, *M. louchuanensis*, *M. sanganhensis*, *M. ordosianus mentougounensis*, *M. baotouensis* and *Cervus candensis mongoliae* Gaudry or *Cervus mongoliae* Gaudry, 1872 (Zdansky, 1928; Young, 1932; Vislobokova, 1990; Vislobokova and Hu 1990; Xue and Zhang, 1991). Several of these names are most probably synonyms. Both *S. pachyosteus* and *S. flabellatus* are based on material from Zhoukoudian and "*mongoliae*" might be the same as *S. ordosonianus*. Here we treat three forms and briefly discuss a fourth. Descriptions of these species have been published: of *Sinomegaceros konwanlinensis* from Gongwangling by Hu and Qi (1978), of *Sinomegaceros pachyosteus* from Zhoukoudian by Zdansky (1925, 1928), Young (1932) and Teilhard de Chardin and Pei (1941), of *Sinomegaceros yabei* from Japan by Shikama and Tsugawa (1962) and Otsuka and Shikama (1977) and of *Sinomegaceros tadzhikisanis* by Vislobokova (1988).

At present, there are two universally recognized European or west Eurasian species that belong to Azzaroli's "*M. giganteus* group" and there are various other forms that are not completely identical to the two universally accepted species:

(1) The species *M. giganteus*, type species of the genus, had a geographical distribution that ranged from Ireland and Spain to Lake Baikal (Lister, 1994; R.D. Kahlke, 1994, 1999). Many other names have been proposed for deer that at present are included in this species and some of these names might be used as subspecific names for well defined morphotypes (van der Made, 2006).

(2) The species *Megaloceros savini* is the only other European species of the "*M. giganteus* group", that at present is included in the genus *Megaloceros*, while occasionally it is placed in the genera *Praedama* and *Dolichodoryceros* (Kahlke, 1969; Azanza & Morales, 1989).

(3) Material from Libakos assigned to "*Eucladoceros*? sp. indet." and "Cervidae gen. et. sp. indet. (Steppen-/Riesenhirsch Formenkreis)" (Steensma, 1988) represents another giant deer with palmate brow tine.

(4) Remains from various localities from Madrid, that have been assigned to *Praedama*, *Cervus* and *Dama* (Andrés and Aguirre, 1975; Sesé and Soto, 2002) belong to a small form close to *M. savini*.

(5) Cueva Victoria yielded remains that were assigned to *M. savini* (Carbonell et al., 1981), but which are different. The age of the locality is controversial. Initially it was placed in the Middle Pleistocene (Pons-Moyà and Moyà-Solà, 1979), but later its age was estimated to be between 0.7 and 1.5 Ma (Carbonell et al., 1981), around 1.2–1.3 Ma (Agustí et al., 1987), as young as 0.5 Ma (Crégut-Bonnoure,1999) and at present most seem to accept an age around 0.8–0.9 Ma, though various authors have suggested that there may be fossils of more than one age (Sesé and Sevilla, 1996, p. 281; Crégut-Bonnoure,1999). The presence of a large *Dama* with perfectly palmate antler suggests an age at least as young as indicated by Crégut-Bonnoure (1999). Some *Megaloceros* antlers were described and figured by Carbonell et al. (1981) and Gibert Clols (1985), the rest of the material has not been described yet.

Table 1
The eight species and subspecies of giant deer with palmate brow tine, that are currently recognized in East Asia, and which are either placed in the genus *Megaloceros* or *Sinomegaceros*. Most of the fossil localities are situtated in China north of the Yangtze River

Taxon	Early Pleistocene	Middle Pleistocene	Late Pleistocene
Sinomegaceros konwanlinensis	*		
Sinomegaceros flabellatus		*	
Sinomegaceros sangganhoensis		*	
Sinomegaceros luochuanensis		*	
Sinomegaceros pachyosteus		*	
Sinomegaceros baotouensis			*
Sinomegaceros ordosianus ordosonianus			*
Sinomegaceros ordosianus mentougouensis			*
Sinomegaceros sanguronensis		*	
Sinomegaceros yabei		*	

2. Material and methods

Giant deer fossils from different localities were studied and data on other samples were collected from the literature (Figs. 2 and 3). When data are used in this paper, a bibliographical reference or an acronym is given. The acronym indicates either the institute were the fossils or recent bones and teeth were studied, or where they are presently kept:

AUT	Aristotle University of Thessaloniki
CIAG	Centre d'Investigacions Arquelògics de Girona.
FASMN	Römisch-Germanisisches Zentralmuseum, Forschungsinstitut für Vor-und Frühgeschichte, Forschungsbereich Altsteinzeit Schloss Monrepos, Neuwied.
HMV	Historisches Museum, Verden.
HUJ	Hebrew University, Jerusalem.
IGF	Istituto di Geologia, Firenze.
IPH	Institut de Paléontologie Humaine, Paris.
IPS	Instituto de Paleontología, Sabadell.

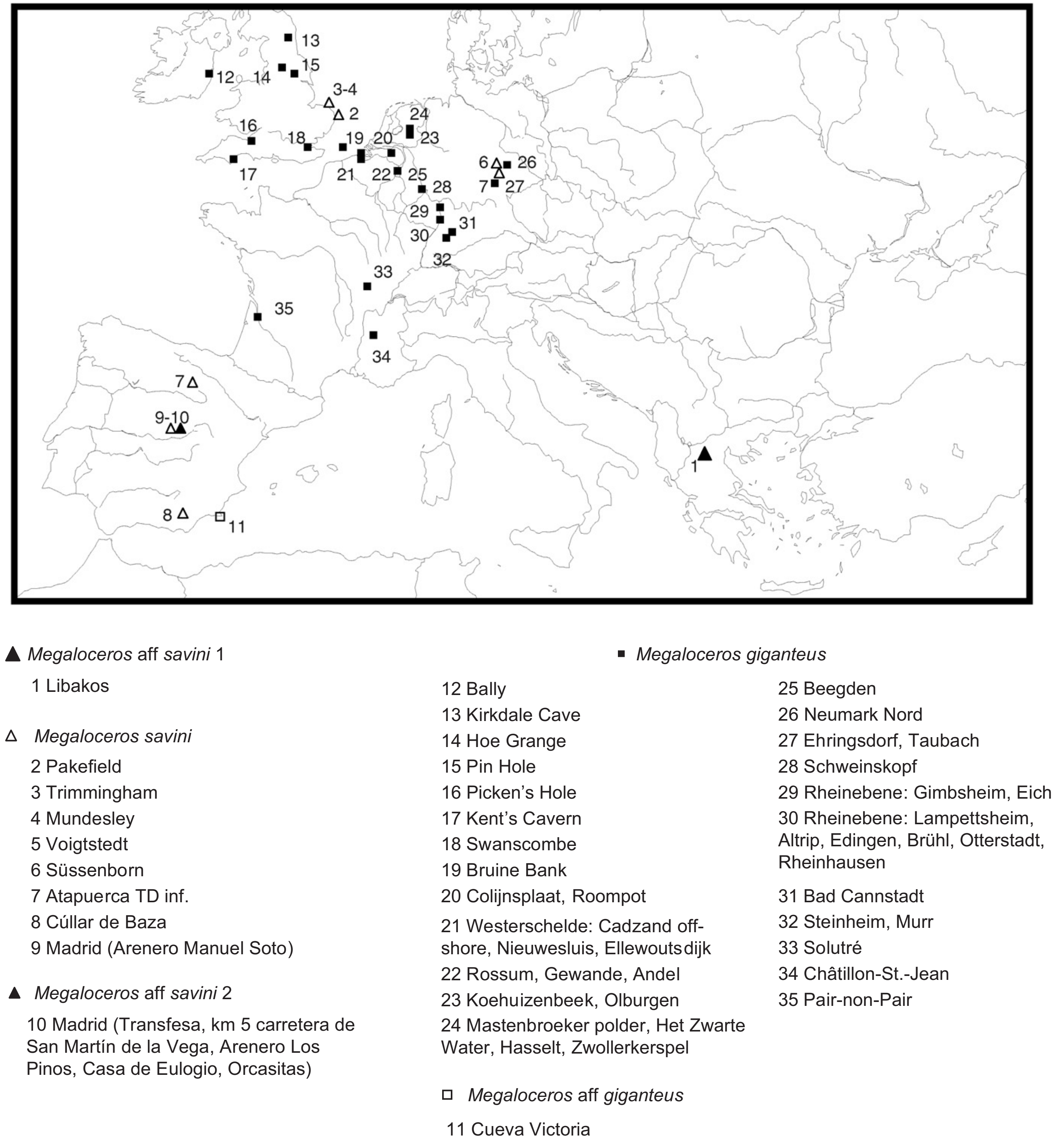


Fig. 2. The geograpic position of the *Megaloceros* localities mentioned in the text. For more detail on the Dutch localities see van der Made (2006).

IQW	Institut für Quartärpaläontologie, Weimar.
IVAU	Instituut voor Aardwetenschappen, Utrecht.
IVPP	Institute for Vertebrate Paleontology and Paleoanthopology, Academia Sinica, Beijing.
KU	Kagoshima University, Kagoshima.
LPT	Laboratoire de Prehistoire de Tautavel, Université de Perpignan.
LVH	Landesmuseum für Vorgeschichte, Halle.
MAC	Museo de Arqueología de Cartagena.
MAN	Museo Arqueológico Nacional, Madrid.
MAR	Museo Arqueológico Regional, Alcalá de Henares.
MB	Museo de Burgos.
MCP	Musée Crozatier, Le Puy-en-Velay.
MNCN	Museo Nacional de Ciencias Naturales, Madrid.
MNHN	Muséum National d'Histoire Naturelle, Paris.

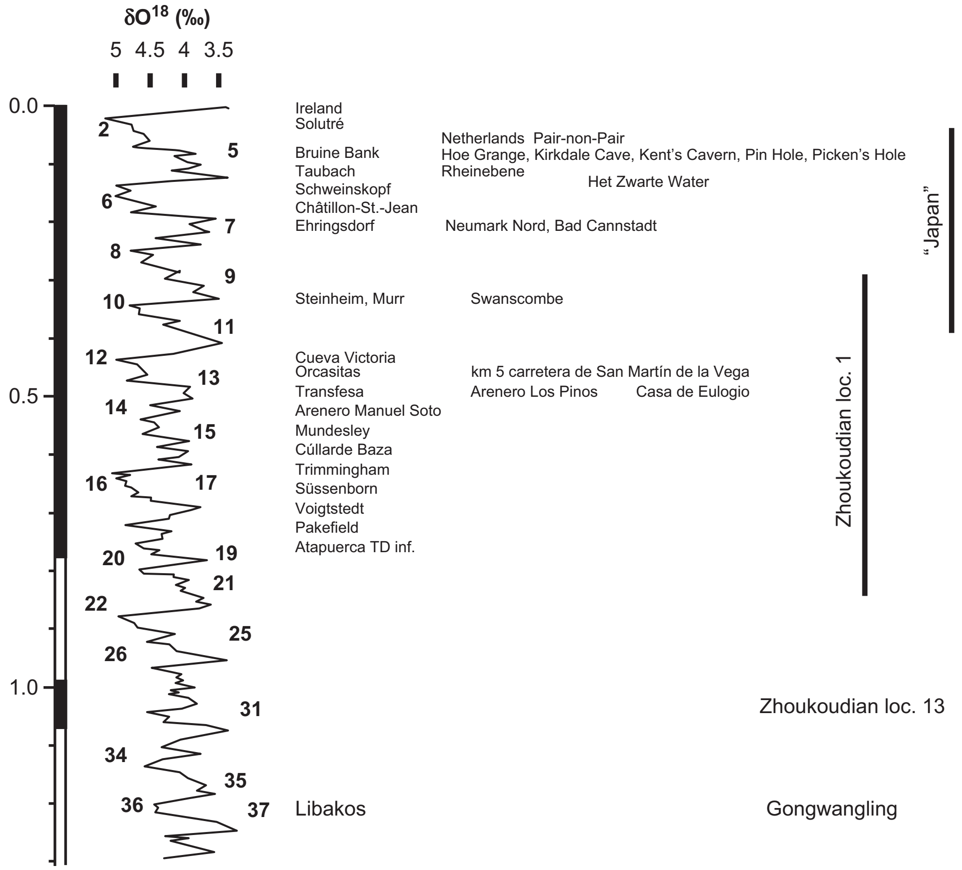


Fig. 3. The approximate chronological position of the localities studied, largely after Lister (1994), van der Made (2001, 2005b, 2006) and van der Made et al. (2003). "Netherlands" includes the Dutch localities listed in Fig. 2, save for Het Zwarte Water and Bruine Bank (Brown Bank) in the North Sea. Bars give the temporal distribution of *S. yabei* in Japan and the range covered by locality 1 of Zhoukoudian.

MRA	Museum Requien, Avignon.
MSI	Museo de San Isidro, Madrid.
MUB	Medical University, Baku.
NKUA	National and Kapodistrian Universtiy of Athens.
NHM	Natural History Museum, London.
NMM	Naturhistorisches Museum, Mainz.
NMMa	Natuurhistorisch Museum, Maastricht.
NMP	National Museum, Prague.
NNML	Nationaal Natuurhistorisch Museum, Leiden.
PIN	Palaeontological Institute, Moscow.
SMNK	Staatliches Museum für Naturkunde, Karlsruhe.
SMNS	Staatliches Museum für Naturkunde, Stuttgart.
TUC	Technische Universität Clausthal, Insitut für Geologie und Paläontologie.
UCM	Universidad Complutense, Madrid.
ZMA	Zoölogisch Museum, Amsterdam.
ZSM	Zhoukoudian Site Museum.

A number of measurements are used here, that will be used repeatedly in following papers. In this sense, they are "standard" measurements, but in several cases differ slightly from the measurements taken by earlier authors, including some, which are widely cited. Therefore, it is indicated here how the measurements were taken, and why they ware taken in this way. The measurements were taken with callipers and are given in mm, unless indicated otherwise. They are indicated with acronyms, which are used in Figs. 4 and 5 and which are listed at the end of this section.

The measurements on the antlers were taken as indicated in Fig. 3. All these measurements are along straight lines. It is common practice to measure the lengths of tines or the circumferences of the burr and pedicle along curved lines following the bone surface. Such measurements are cumbersome to take and are probably more difficult to reproduce. In addition, they take more time, which is often limited if one is travelling to collect data. Here straight measurements, that can be taken with callipers, are preferred. The circumference (Lister, 1994; Pfeiffer, 1997) or antero-posterio (DAPr) and transverse (DTr) diameters of the burr are frequently given (Heintz, 1970). However, the burr is often eroded or broken (e.g. Pfeiffer, 1997). It is better to use the diameters of the antler just above the burr (DAPb and DTb). The position of the bifurcation of the brow tine and main beam is often measured from the upper surface of the burr (e.g. Heintz, 1970), however, the same measurement from below the burr is probably more easy to reproduce. Though both measurements were taken, those taken from below the burr are used in the graphs (Figs. 11

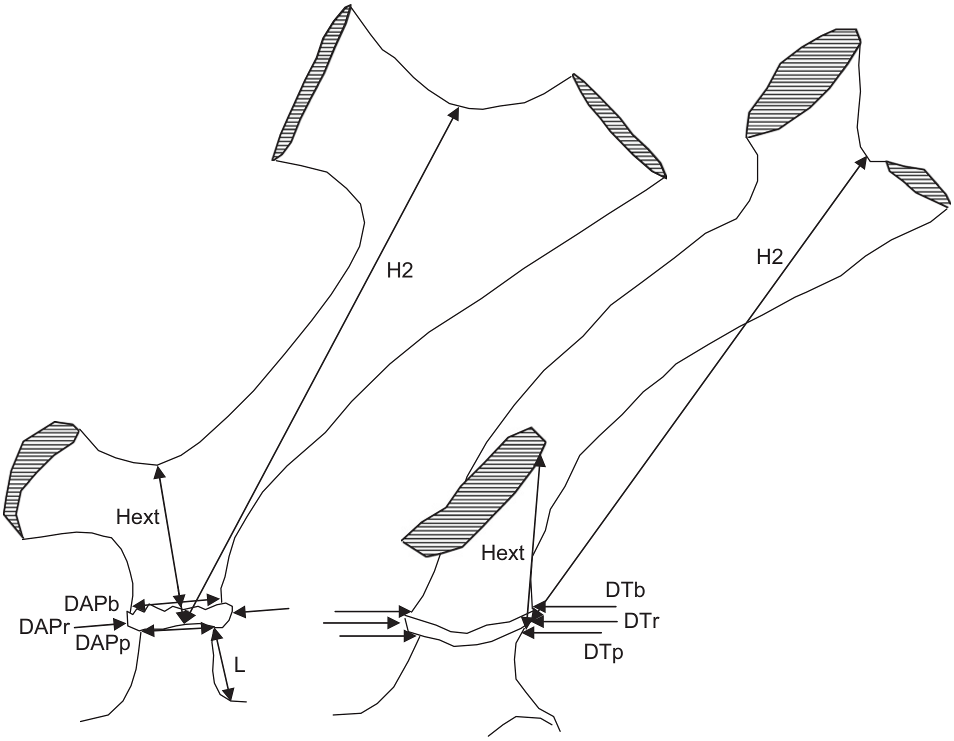


Fig. 4. The way of measuring the antlers. See section on material and methods.

and 12). These measurements are often taken at the medial side (e.g. Heintz, 1970; here called Hint). However, the antler usually flares out laterally and the bifurcation is situated above the lateral side of the burr. The height above the burr can thus be measured more easily at the lateral side. This measurement is probably also more easy to reproduce, resulting in less variability of the samples measured. The measurement is taken as the shortest distance from below the burr to the bifurcation. This may be in the middle of the burr (if seen from the side) or a little anterior to this point. The measurement should be more or less perpendicular to the plane of the burr. In wide antlers with a very low bifurcation, it should be avoided to incline the callipers much in the transverse plane and preferentially callipers with an adjustable beak should be used. The height of the second (*H*2) and following tines (*H*3, *H*4, …) is measured in the same way, but always from below the burr and at the lateral side. The height of the separation of the brow tine and main beam is treated here in particular. The different sizes of the species and specimens treated here, obscure a pattern of a decrease in height of this separation. In an attempt to "remove" size, the index 100 Hext/DAPb is used.

While in proboscideans and arvicolids, enamel thickness is commonly measured, this is not so common in cervids. Nevertheless, enamel thickness varies greatly among the different cervid species, which probably is related to the diet of the species. Here enamel thickness is measured as indicated in Fig. 5. The measurement and the index 1000 Ta/DTa was defined and applied to the suid dentition (van der Made, 1996, 2004). The measurement and index can be taken at the first (Ta) and second lobe (Tp) of each molar. These measurements are not necessarily identical in each tooth, but if homologous measurements are compared, the same pattern is observed. The same is true for upper and lower molars (in uppers, the *T* values are measured at the buccal side). In general, the index, or relative enamel thickness increases from M1 to M3. However, some species have relatively thick enamel in the first molars and only slightly thicker enamel in the second and third molars, where as in others the cline is more marked. It seems thus, that for a full characterisation of this feature in a species, the values of the different molars have to be given, preferentially including the index 100 Ta/DTa of all lower molars. The enamel thickness is usually measured at the occlusal surface. The highest values for T are measured in teeth with just enough wear to show the dentine and the lowest values in teeth with nearly all enamel worn away. However, the changes in enamel thickness are greatest near the tip and near the base of the tooth, while there is relatively little variation in enamel thickness in the large intermediate part. This is especially so in very high crowns. Other tooth measurements were taken according to van der Made (1989).

Pachyostosis is a common feature in giant deer and is primarily noted in the thick mandible. Frequently the character is treated in a qualitative way, describing the presence of the feature and/or giving drawings of the section of the mandible (Zdansky, 1928; Kahlke, 1975, 1977). Kahlke (1965, 1969, 1997, Table 60, Fig. 36) gave sections and measurements, taken below the molars. In some cases the depth is measured at the lingual side

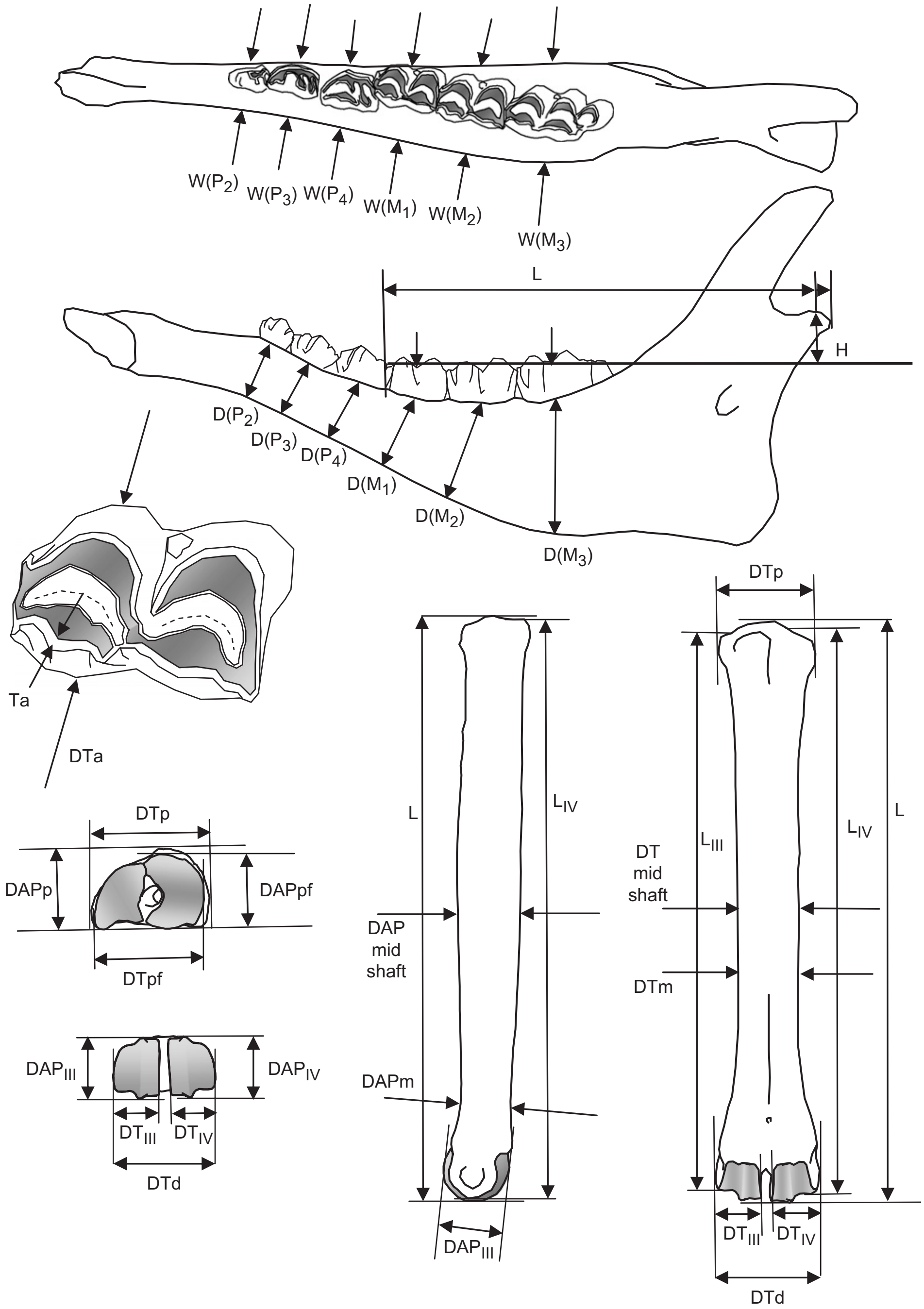


Fig. 5. The way of measuring teeth, mandibles and metapodials. See section on material and methods.

(Kahlke, 1997), in others at the buccal side (Zdansky, 1925). Young (1932) gave measurements of many specimens taken before the P_2 and below the M_3, but did not indicate whether the depth was measured at the lingual or buccal side (which gives different results). Lister (1994, Fig. 17) compared mandible width with M_3 length. Here, the depth is measured at the lingual side of the mandible, below the middle of each cheek tooth and the width is measured in the same places perpendicular to the depth (Fig. 5). An index 100 D/W is calculated, as was done by Young (1932) (though, for the reason indicated above, we do not know whether the values are comparable). Because, the size and shape of the mandible changes much until adulthood is reached, here, only measurements on mandibles of adults are used, with M_3 or the premolars fully erupted.

Differences in the position of the mandibular condyle between the different species of giant deer were observed, which might give information on diet in conjunction with other characters (such as enamel thickness). Such differences are generally observed qualitatively, but quantification results in more precise observations. Therefore a way to measure the position of the condyle with respect to the teeth row is defined here. The ''occlusal surface'' is taken here as a plane (or line) that passes through the lower most parts of the transverse valleys of the first and third molars, as seen in side view. The elevation of the condyle is the distance of the upper surface of the condyle to this line or plane. The distance of the condyle behind the anterior edge of the M_1 is measured as the projection of the condyle on that line. Two measurements are taken, one the projection of the highest point of the condyle and the other on the projection of the posterior edge of the condyle. The latter value is used here. In ruminants, these places nearly coincide, but in other animals (like suids), there is much more difference. The values describe the condylar position relative to just one point in the tooth row, but the method of measuring can be applied to any point in the tooth row. The measurements can be taken conveniently placing the mandible with the lingual side on millimetre paper and observing the reference points strictly vertically.

The robusticity of the cannon bone is a character that is often used in cervid and bovid systematics. The metacarpal is used more often than the metatarsal, though the reason for this is rarely or never stated. Our observations suggest, that the metacarpal shows more variation in robusticity than the metatarsal. This might be so, because the metacarpals tend to support a greater portion of the body weight, while the metatarsals are more important in the propulsion. Usually, length is compared to proximal (e.g. Daxner, 1968) or distal width (e.g. Daxner, 1968; Lister, 1994; Kahlke, 1997; Sher, 1997; van der Made, 1999a, 2006), the minimal width of the shaft (Daxner, 1968; Moyà Solà, 1987), or the width of the shaft at mid height, but never to the antero-posterior diameter. Because of the features used to "sex" bison metacarpals (Schertz, 1936), we suspect, that in cervids minimal (DTm) or mid shaft width is more subject to sexual bimodality than distal and proximal width, producing "noise" that obliterates differences between species. Here we use distal width or DTd. The comparisons between length and width are either made in bivariate plots comparing the length to one of the measurements of the width (e.g. Lister, 1994; Kahlke, 1997; van der Made, 1999a, 2005a, 2006), or to an index of robusticity (Daxner, 1968; Sher, 1997). Alternatively, the indices of robusticity are compared directly (e.g. van der Made, 2005a).

The measurements are indicated by the following abbreviations:

$D(P_2)$	depth of the mandible, or shortest distance between the upper and lower edges of the mandible (but not measured necessarily perpendicular to the upper or lower edge), measured at the lingual side below the middle of the P_2 (or P_3, P_4, …).
DAP	antero–posterior diameter.
DAPb	DAP measured near the base of the crown, or DAP of an antler measured just above the burr.
DAPmini	minimal DAP of the shaft of a metapodial.
DAPp	DAP of the proximal part of a bone.
DAPpf	DAP of the proximal articular facet of a bone.
DAPr	DAP of the burr of an antler.
DAP III	DAP of the distal articulation of the third metapodial.
DAP IV	DAP of the distal articulation of the fourth metapodial.
DT	Transverse diameter.
DTa	DT of the anterior lobe of a tooth.
DTb	DT of an antler measured just above the burr.
DTd	DT of the distal part of a bone.
DTmini	minimal DT of the shaft of a metapodial.
DTp	DT of the posterior lobe o a tooth, or DT of the proximal part of a bone.
DTpf	DT of the articular facet of the proximal part of a bone.
DTr	DT of the burr of an antler.
DT III	DT of the distal articulation of the third metapodial.
DT IV	DT of the distal articulation of the fourth metapodial.
H	height of the mandibular condyle above a line that passes through the deepest points of the transverse valleys of the first and third molars.
Hext	height of the bifurcation of the brow tine and main beam of the antler above the lower/upper part of the burr, measured at the lateral side.
Hint	height of the bifurcation of the brow tine and main beam of the antler above the lower/upper part of the burr, measured at the medial side.
H2	height of the bifurcation of the second time and main beam of the antler, measured analogous to Hext
L	length of a bone or of the pedicle. Distance from the anterior border of the M_1 to the projection of the highest point of the mandibular condyle, or the posterior edge of the mandibular condyle, on a line that passes through the deepest points of the transverse valleys of the first and third molars.
L3, L4	alternative lengths of the third and fourth metapodials.
Ta	enamel thickness measured at the lingual side of the metaconid or the buccal side of the paraconid.
$W(P_2)$	width of the mandible, measured below the middle of the P_2 (or P_3, P_4, …) and perpendicular at the depth D.

3. The characters studied

3.1. Palmate brow tine

The imporance of the palmation of the brow tine was recognized by Azzaroli (1953), who divided the genus "*Megaceros*" (= *Megaloceros*) in two groups, the "*M. verticornis* group", with brow tine with round section, and the "*M. giganteus group*", with flattened brow tines. The implicit assumption was that the character is a common derived character.

The giant deer compared here have all palmate brow tines (Figs. 6–9). Deer with palmate brow tines appeared at the end of the Early Pleistocene in both west (Libakos) and east Eurasia (Gongwangling), around approximately 1.2 Ma ago. The origin of the palmate brow tine is not known. Material from Kuruksai was assigned to *Sinomegaceros* (Vislobokova, 1988, 1900). Clear palmations are not known from this locality, though also *Elaphurus* is cited from there and some of the brow tines have some degree of flattening and even incepient bifurcation. This locality is Late Pliocene in age, close to 2 Ma Bp. Other deer with a brow tine that shows a tendency to become flattened or bifurcated include *Elaphurus*, which, as stated above is present in Kuruksai (Sharapov, 1986; Vislobokova, 1988, 1990) and *Arvernoceros ardei* from Late Pliocene localities like Étouaires and Villaroya, with ages between some 2.5 and 3.5 Ma (Fig. 9-1; Heintz, 1970).

3.2. *Orientation of palmate brow tine*

Shikama and Tsugawa (1962) recognized the importance of the orientation of the plane of the palmation of the brow tine, and measured the strike of these planes. This is cumbersome to measure, but measuring strike and dip with respect to the plane and antero-posterior axis of the burr might be a good method to quantify this character and to study its variability and changes. The measurements could be plotted in a stereographic projection. We classified the orientation of the brow tine in a qualitative way: it is oriented transversely, it is oriented antero-posteriorly with medial or lateral dip, or it may be vertical as in *S. ordosonianus*.

The brow tines of *Megaloceros* aff. *savini* from Libakos (Fig. 7-3) and Madrid (Fig. 7-6), *M. savini* (Figs. 7-1, 8-1, 8-5) and *S. konwanlinensis* (Fig. 7-7) dip medially, the brow tines of *M. giganteus* are oriented horizontally or dip laterally (Fig. 6-2), and those of *S. pachyosteus* (Figs. 8-1, 8-2, 8-3) and *S. yabei* (Fig. 9-3) are oriented vertically and transversely. Occasionally the brow tines in *S. yabei* may be oriented more antero-posteriorly, resembling *Sinomegaceros ordosonianus.* The latter species (which is not further considered here) has brow tines that are oriented vertically and antero-posteriorly (Teilhard de Chardin and Pei, 1941, Fig. 7-1). At least, this is what is observed in antlers of adults.

Antlers of not yet fully adult *M. giganteus* are recognizable by their small size and, if they are complete, a relatively simple distal part and a well developed second tine. The antlers of very young individuals have brow tines that dip medially (Fig. 6-3), as in *M. savini*, but the specimens retain other characters that are typical of *M. giganteus*, such as the low bifurcation.

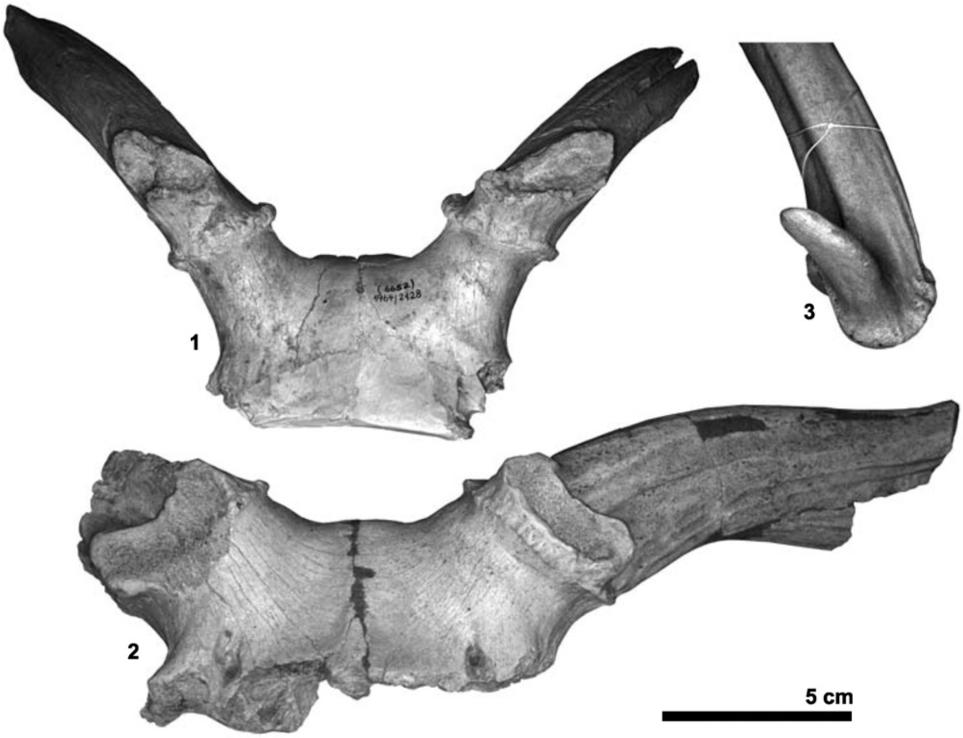


Fig. 6. Orientation of the brow tine: inclined medially in *M. savini* (1) and laterally in *M giganteus* (2). Though in both specimens the brow tines are broken off at the base, the orientation they have is seen well. In juvenile *M. giganteus* (3), the brow tine is inclined medially, as in *M. savini*: (1) *M. savini* from Süssenborn IQW no. 1964/2128 (6652); (2) *M. giganteus* from Steinheim an der Murr, SMNS no. 11962; (3) *M. giganteus* from Rheinhausen (Rheinebene) SMNS no. 6717.8.11.80.4 (Fig. 6-3 not to scale).

Fig. 7. Morphology of the distal palmation and "second tine" in different species of giant deer: (1) *M. savini* from Atapuerca Gran Dolina (precise level unkown), MB AT-Y-201: (a) antero-superior view, (b) medial view; (2) *M. giganteus* from Otterstadt (Rheinebene), SMNS 6616.5.5.84.15: medial view; (3) *Megaloceros* aff. *savini* from Libakos, TUC E/S:L-Cg:g-1: (a) lateral view, (b) anterior view; (4) *Megaloceros* from Cueva Victoria, MAC CV-BL1-250 and CV-BL1-251: lateral view; (5) *M. savini* from Trimmingham, NHM M6093 (Savin 112), lateral view; (6) *Megaloceros* aff. *savini* from km 5 carretera San Martín de la Vega (Madrid), MSI API/ 59-119790-2: medial view; (7) *S. konwanlinensis* from Gongwangling, IVPP v2944.4: (a) anterior view, (b) lateral view. The scale represents bar 11 cm for Fig. 2, and 5 cm for the remaining figures.

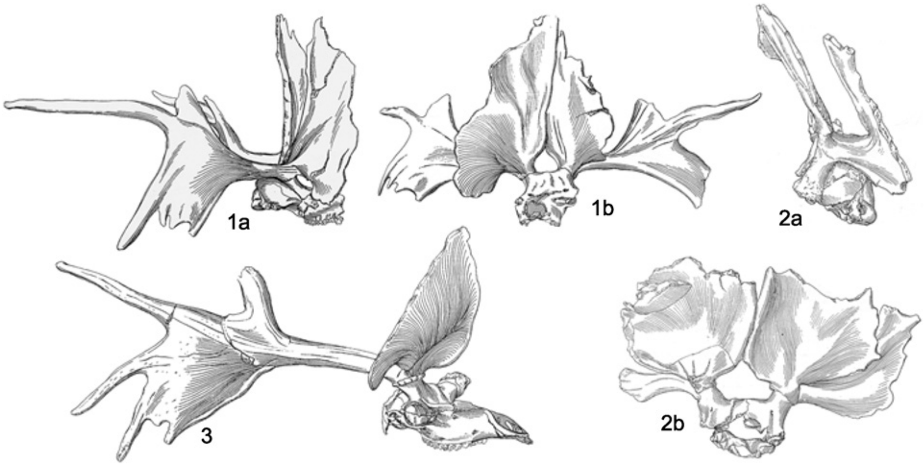


Fig. 8. *Megaloceros pachosteus* from Zhoukoudian loc. 13: (1) skull 1, right lateral and anterior view; (2) skull 7, left lateral and anterior views; (3) skull 2, right lateral view. All figures from Teilhard de Chardin and Pei (1941).

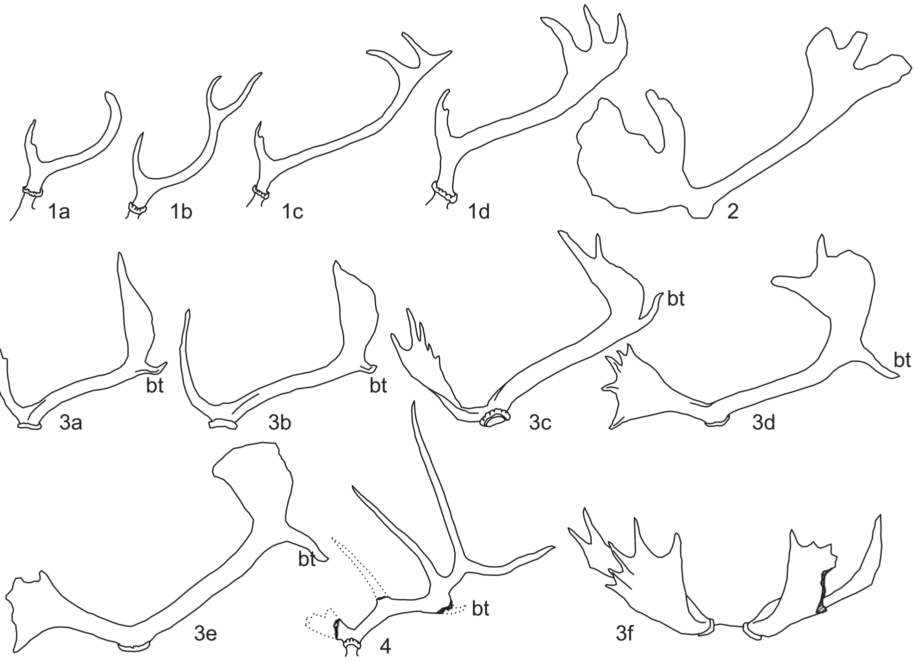


Fig. 9. Line drawings of the antlers of selected deer: (1) *A. ardei* four ontogenetic stages after Heintz (1970, Figs. 302, 305, 315, 295) and based on: (a) a specimen from Étouaires, (b) NHM 34590 from Étouaires, (c) hypothetical stage, (d) a specimen figured by Depéret (1884); (2) *S. konwanlinensis* from Gongwangling after Hu and Qi (1978); (3) *S. yabei* from Gunma after Shikama and Tsugawa (1962); (a–e) lateral views, (f) frontal view; (4) *M. savini* from Süssenborn (IQW 1964/1937, Süss 7075); the stippled lines are reconstructions of the parts that are lacking. Possible analogues of the "back tine" are indicated with "bt"; see discussion in text.

An antler that was interpreted to have been used as a percutor, was described from Cueva Victoria as *M. savini* (Carbonell et al., 1981). A similar antler was studied in the IPS. It has a brow tine that is inclined medially as in *M. savini*, but it differs from that species in that the bifurcation is situated much higher. These specimens are from the initial collections. Subsequent systematic excavations, lead by J. Gibert, yielded a much more complete antler, that has a brow tine that is dipping laterally, as in *M. giganteus*, but again its bifurcation is situated very high. The fact that both specimens are particular in having a bifurcation that is much higher than in *M. savini*, suggest, that the two specimens belong to the same species. It is not clear, whether the different orientations of the brow tines indicate ontogenetic variation, or variation across a population of adults.

3.3. Height of the bifurcation brow tine-main beam

An interesting feature is the position of the origin of the brow tine, which best can be quantified by measuring the height of the bifurcation between brow tine and main beam. There are great differences among the Cervidae. While the Cervinae tend to have lower bifurcations, the

Odocoilinae tend to have very high bifurcations (think of *Capreolus*) and some Late Miocene cervids had very high bifurcations (Azanza Asensio, 2000). While in the Middle and early Late Miocene *Euprox* a gradual increase in the height of the bifurcation can be observed, in the Plio-Pleistocene *Dama*-like deer there is a decrease in height (van der Made, 1999a). The meaning of these changes is not clear, though it seems likely, that they have to do with offensive or defensive behaviour and/or visual display.

Fig. 10 shows the height of the bifurcation in the different giant deer, as indicated by the plain measurement Hext. *M. giganteus* tends to have the lowest values, followed by *S. pachyosteus* and possibly *S. yabei*, while the early Pleistocene *S. konwanlinensis* and *M.* aff. *savini* from Libakos have the highest values. Overall, there is a decrease in both west and east Eurasia. However, the smallest forms in this study approach *Dama* in size. There is thus a wide range in sizes, and therefore the index 100‘ Hext/DAP is used in Fig. 11. The overall pattern is similar, save for that the observed trend becomes even more clear and that some of the samples are better separated, with *M. savini* with values intermediate between the Early Pleistocene samples and *Megaloceros gianteus*. On average, *Megaloceros* aff. *savini* and *S. pachyosteus* are situated between *M. savini* and *M. giganteus*. The general tendency of decrease of the values in both east and west is confirmed, which suggests the plesiomorphic acquistion of brow tines with a lower point of origin, but alternatively, the feature might have evolved in parallel.

The two values from Cueva Victoria are relatively high, though both are approximate. One of the specimens (indicated with an inverted triangle) has the morphology of *M. savini*, with a medially inclined brow tine. This is one of two specimens from the earliest collections that were assigned to *M. savini* and which were interpreted as showing signs of being worked by early *Homo* (Carbonell et al., 1981; Gibert Clols, 1985). The other specimen in the graph is from later excavations lead by J. Gibert and its provenance is known, there are many other *Megaloceros* specimens in this collection, which comes from different parts of this large cave. These remains seem to indicate the same form, even though they come from different parts in the cave. The antler from this collection is more complete and has a brow tine with lateral inclination, as in *M. giganteus*, nevertheless its bifurcation is high.

3.4. *The presence of a "Second tine"*

In *S. pachyosteus* (Fig. 8), *S. konwanlinensis* (Fig. 9-2) and *S. yabei* (Fig. 9-3), there is never a "second" tine

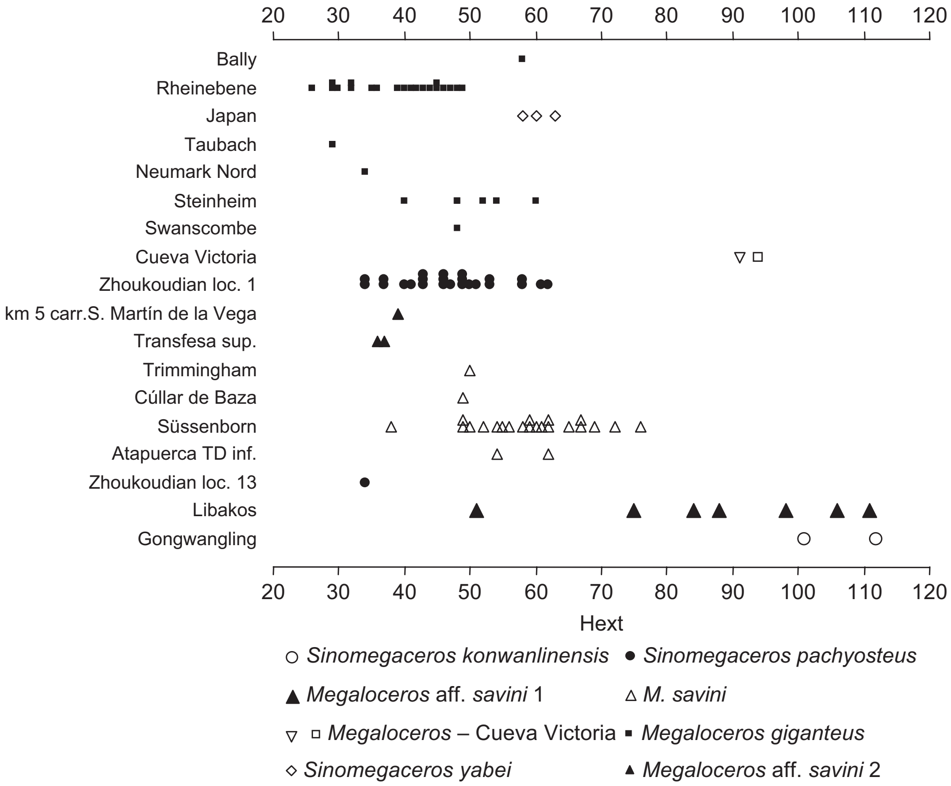


Fig. 10. Height of the bifurcation of the brow tine and main beam above the burr (Hext). The localities are arranged approximately from old (bottom) to young (top): Gongwangling (IVPP), Libakos (TUC), Zhoukoudian loc. 13 (ZSM), Atapuerca TDinf (MB), Süssenborn (IQW), Cúllar de Baza I (MNCN), Trimmingham (approximate value; NHM), Transfesa superior (MAR), km 5 carretera de San Martín de la Vega (MSI; two specimens with the same value), Zhoukoudian loc. 1 (ZSM), Cueva Victoria (approximate values; IPS, MAC), Swanscombe (NHM), Steinheim (SMNS), Neumark Nord (LVH), Taubach (IQW), Japan (limestone quarry at Isa town and an unkown locality, KU), the Rhine valley (SMNS), Bally (NNML).

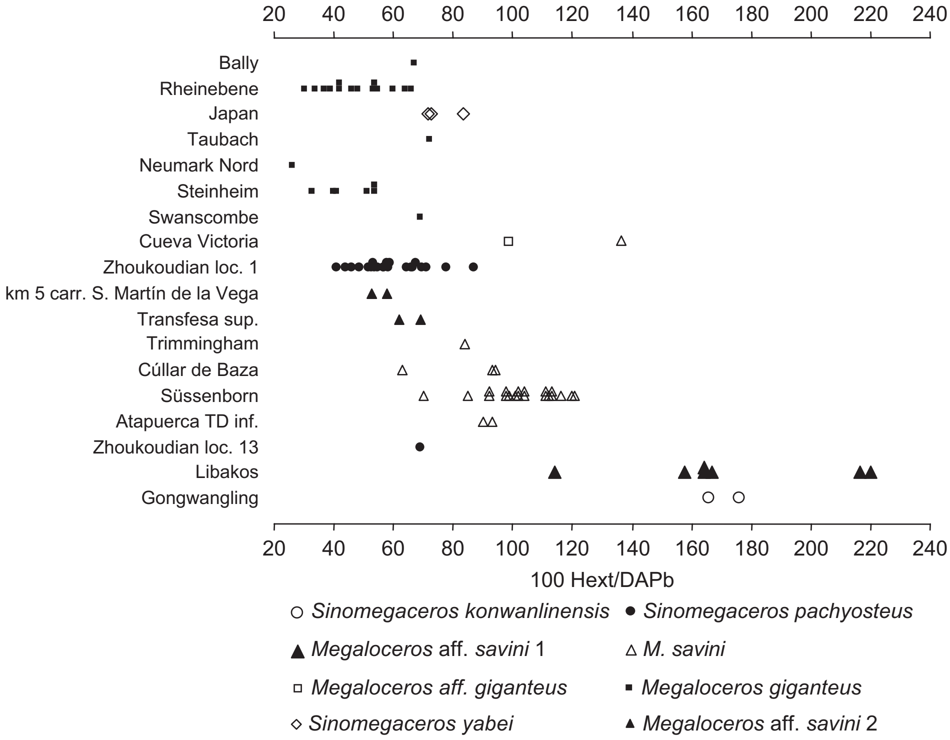


Fig. 11. Height of the bifurcation of the brow tine and main beam above the burr, as indicated by the index 100 Hext/DAPb. Provenance of data as in Fig. 5. The highest of the two values of km 5 carretera San Martin de la Vega is an approximate value.

between brow tine and distal palmation, even though the main beam may be very long. In *Megaloceros* aff. *savini* from Libakos (Fig. 7-3) and Madrid (Fg. 6-6), *M. savini* (Figs. 7-5, 9-4) and *Megaloceros* from Cueva Victoria (Fig. 7-4), there is an anteriorly directed tine that arises from the main beam at some distance of the brow tine. Behind that "second" tine, the main beam continues. In well developed *M. giganteus* antlers, this "second" tine is not always recognizable. In antlers, that presumably did not belong to fully adult individuals, the palmation has a lesser development and a "second tine" is clearly present (Fig. 9-2). Probably, this tine became incorporated in the well developed palmations.

In *M. giganteus*, there is much variation in the distance of the second bifurcation to the burr (H2), and the values of the other species fit easily within this range of variation (Fig. 12). However, if the index 110 H2/DAPb is used, there seem to be some differences between the species, suggestive of a progressive lowering in the geologically younger samples, similar to that observed in first bifurcation. This is what is expected, but more data are needed to confirm the trend.

3.5. Distal palmation

In *M. savini*, there is a "third tine" situated distally of the "second tine", described above, which bifurcates and bifurcates again, resulting in three tines, but not in a palmation (Figs. 7-5, 9-4). The proximal part of this third tine, before bifurcating, may be flattened with a long diameter in the direction of the main beam and a short transverse diameter. This seems to forecast the palmation in *M. giganteus*. In *Megaloceros* from Cueva Victoria, there is a third bifurcation and the anterior tine does not seem to be very large or flattened (this is at the very end of the specimen of Fig. 7-4). This suggests, that there was no distal palmation.

In *M. giganteus*, there is a well developed distal palmation. In specimens that belonged presumably to rather young individuals, there is a small palmate structure that looks like the tines of *M. savini*, but shorter and with the space between the tines filled in with flat bone (Fig. 7-2), and this probably is also the way in which the palmation originated. In these specimens the palmation arises thus from the anterior side of the main beam. Distally of this, the main beam does not continue, save for in a small tine, the "back tine" of Lister et al. (2005) (and called "Dorn" in German). This tine resembles a similar structure in *Eucladoceros* antlers. In *Eucladoceros* there may be several anterior tines, probably reflecting more or less the ontogenetic age of the individual. At the end of the antler, and as a straight continuation of the main beam, there is always such a small tine, which is much smaller than any of the anterior tines. It seems that this is the way how the main beam terminates. This little end of the main beam, resembles a tine in fallow deer antlers, which became directed posteriorly. It seems that both in *M. giganteus* and *Dama*, the palmation developed from the "third tine" and

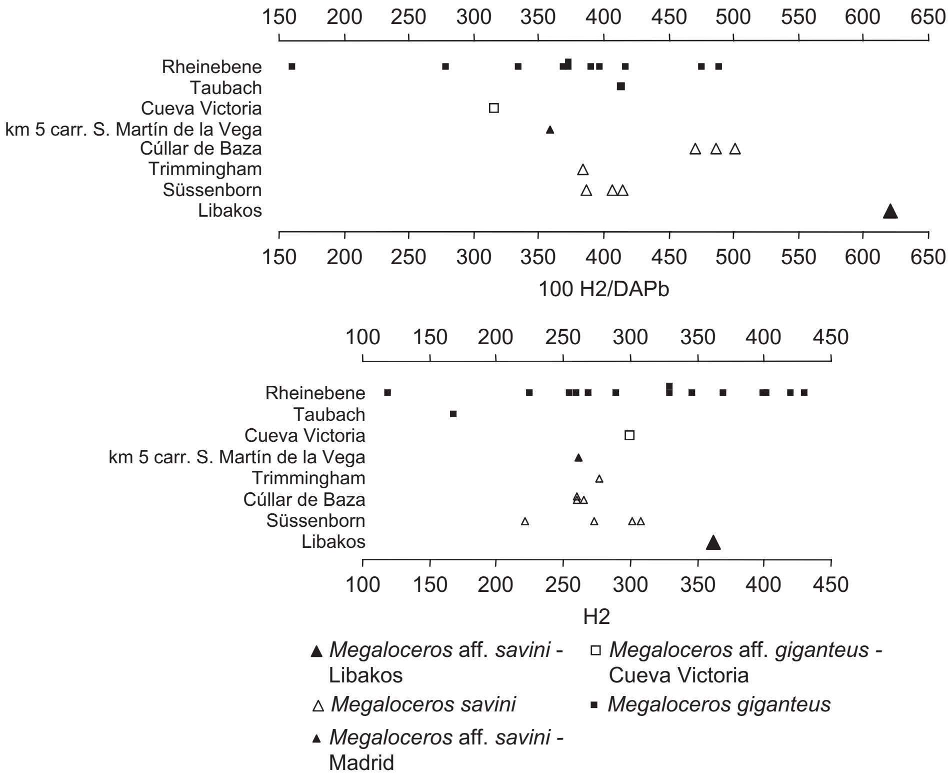


Fig. 12. The position of the second tine, as indicated by H2 and 100 H2/DAPb. Provenance of data as in Figs. 10 and 11.

that distally of this tine, the main beam ended in this small structure. If the palmation is well developed, this little structure becomes incorporated in the palmation and seems directed posteriorly. Whereas in *Dama*, the palmation curves upward and foreward, in *M. giganteus* it is directed anteriorly only in the presumably relatively young individuals (Fig. 7-2) and it is directed upward in geologically early forms (*M. g. antecedens*), but generally it is directed outward and even downward.

In *S. pachyosteus* (Fig. 8) and *S. konwanlinensis* (Fig. 9-2), there is a distal palmation. It is situated at the very end of the main beam, which may be long. The palmation is developed as a continuation of the main beam and does not arise from the anterior side of the main beam. In this, the antlers resemble the antlers of *A. ardei* (Fig. 9-1). The antler of *S. konwanlinensis* has many more resemblances with that species; the long anteriorly curved main beam, the small distal palmation with three points, and a bifurcation that is situated far above the burr.

In *S. yabei* (Fig. 9-3), the palmation is very small and directed upward, as in *S. konwanlinensis*. A peculiarity in *S. yabei*, is that there is a structure that resembles a structure in *Dama dama* and relatively young *M. giganteus*, the so called ‘‘back tine’’, which has been mentioned above. This is suggestive of an origin of the palmation from a tine that was directed anteriorly from the main beam, as inferred in *M. giganteus*. The structure is constant and present in many specimens figured by Shikama and Tsugawa (1962).

3.6. *Pachyostosis—robusticity of the mandible*

Most or all giant deer had ‘‘thick’’ or wide mandibles in comparison to other deer. This is called pachyostosis and, because of the extreme development of the feature, one of the species was named *S. pachyosteus*. The mandibles are thickened because of the deposition of lamellar bone early in adult life (Lister, 1994). As a result the compact bone of the mandibles is very thick. The increased width of the mandibles can easily be observed and this is what is usually noted in the descriptions, though stricktly speaking, a wide mandible is not the same as pachyostosis.

As indicated by the termination ‘‘-osis’’, pachyostosis is a disease in which bone becomes thickened. Since the feature is constant in many species of giant deer, it is clear that in this case it is not the result of a disease, though it remains obscure what was its cause or function. It has been suggested that the feature is related to seasonality and the appearance of cranial appendages that are annually shed (Morales et al., 1992). Cranial appendages appeared at the end of the Early Miocene in many ruminant families, including Cervidae, Palaeomerycidae, Bovidae, Giraffidae and even in Suidae (Gabunia, 1960; Azanza Asensio, 2000). Cranial appendages may either be present in both sexes, or only in the males. In the Cervidae, they are restricted to the males, save in *Rangifer*. The Cervidae are particular in that they shed their cranial appendages, or antlers, annually, though this may not yet have been the case in the very earliest forms. The antlers are grown again each year, initially as cartillage structures, while mineralisation occurs in a very short period lateron. In the Early Miocene, the antlers were small, but later, and certainly in the giant deer, they became very large. If the function of pachyostosis would be temporary storage of minerals, indications of resorption should be found in many mandibles of pachyostose species, but such a phenomenon has not been described. Great differences in the degree of pachyostosis would be expected between males and females, but could not be demonstrated (Lister, 1994). The minerals that may be stored in pachyostose mandibles is small in comparison to the quantities needed for antlers, and there is little indication for pachyostosis in other bones of the giant deer (e.g. Sander and Andrássy, 2006), though pachyostose limb bones have been described in a giraffoid (Morales et al., 1992).

The degree in which additional bone layers are present in the mandible is not easy to quantify, but measurements of depth and width are commonly used to describe the feature and this pragmatic approach is followed here. Some of the results are shown in Fig. 13, where it can be seen that *Capreolus*, *D. dama*, *C. elaphus* and *Alces* represent deer of different sizes with slender mandibles, that is, they are narrow for their depth, while in different species of giant deer, the mandibles are much wider. Given the fact that *Alces* mandibles are as wide as those of many of the giant deer, but much deeper, allometry does not explain the differences. It should also be noted that wide mandibles occur not only in *Megaloceros*, but also in *Eucladoceros*.

The relative width or "robusticity" of mandibles can be described with the index 100 D/W and this is done for the mandible below the M_3 in Fig. 14. The taxa are arranged according to robustity, with *C. elaphus* at the slender extreme and *Sinomegaceros pachyosteus* at the robust extreme. Among the giant deer, *Megaloceros* aff. *savini* from Madrid and *Eucladoceros* have mandibles that are relatively slender, while those of *S. yabei* and *M. giganteus* are more robust, but not yet as much as *S. pachyosteus*.

Fig. 15 shows the robusticity of the mandible below the different cheek teeth in two species of giant deer. Whereas in *M. giganteus*, the robusticity increases from P_2 to M_2 and M_3, in *S. pachyosteus*, it increases till M_1 and from there it decreases till M_3. Mandibles are thus not just robust or slender, but they differ also in the place where maximal robusticity is reached. Further study might reveal whether this reflects a different expression in a more advanced state of the same process, or a fundamentally different process.

3.7. Mandibular condyle

It is common knowledge that there is much variation in the position of the mandibular condyle with respect to the cheek teeth. The physics of mastication are complex and a full discussion is beyond the scope of this paper, however some general principles should be recalled. An elevated condyle results in the tooth row being closed more or less at the same moment over all its length (which is more effective for a ruminant or other herbivore), whereas a low condyle results in a distance between the posterior upper and lower teeth that is markedly less than between the anterior teeth, and the jaws seem to close gradually from the back to the

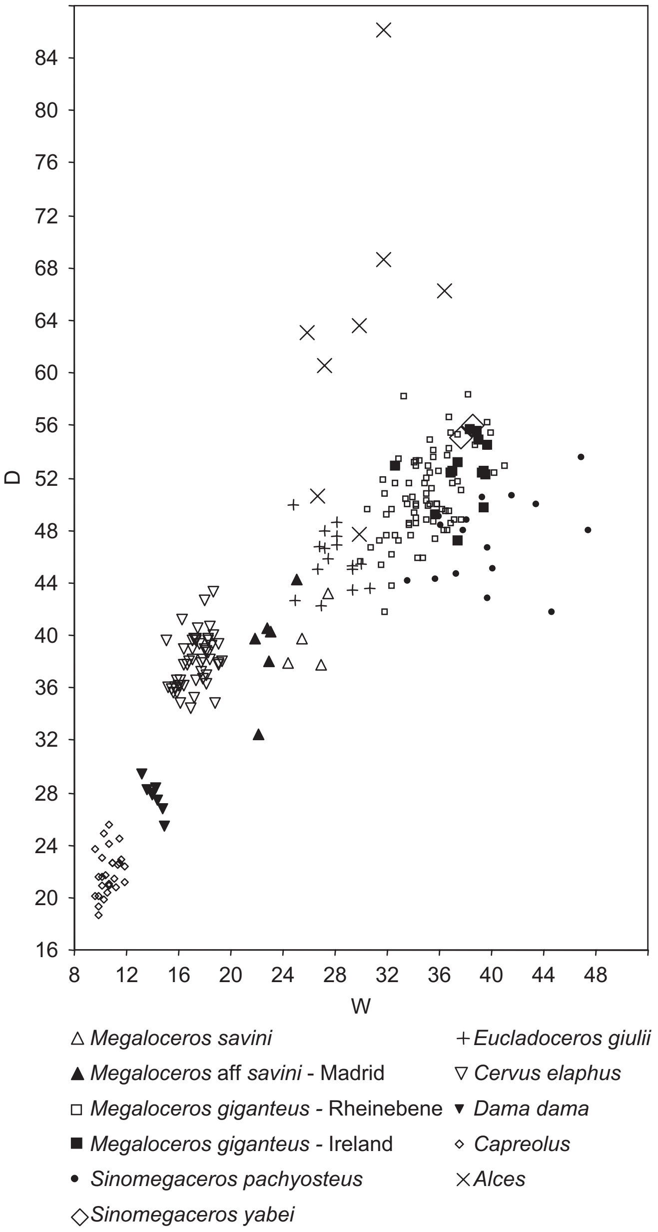


Fig. 13. The size of the mandible below M_3 (D is depth and W is width) compared: recent *Capreolus capreolus* from Spain (MNCN), recent *D. dama* from Spain (MNCN), recent *C. elaphus* from Spain (MNCN), *Alces* from the Pleistocene of the Netherlands (NNML) and the Rheinebene (Rhine valley; NMM), *E. giulii* from Untermassfeld (IQW), *M. savini* from Mundesley (NHM) and Arenero de Manuel Soto (Madrid; MSI), *Megaloceros* aff. *savini* from Casa de Eulogio (MSI), Arenero de Nicomedes (MSI), Oxigeno (MAN), Transfesa (MNCN), Madrid collection Santa Olalla (MAN), *M. giganteus* from Ireland (NHM), and from the Rhine valley (NMM), *S. pachyosteus* from Zhoukoudian loc. 1 and loc. 13 (ZSM, IVPP, IQW, PIN, NKUA), and *S. yabei* from a limestone quarry at Isa town, Japan (KU).

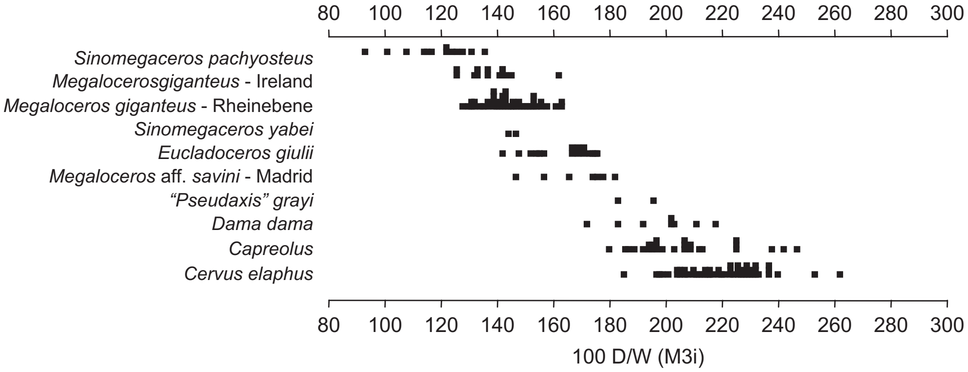


Fig. 14. Robusticity of the horizontal ramus of the mandible below the M_3 as indicated by the index $100\,D/W$. Provenance of data as in Fig. 11; in addition *P. grayi* from Zhoukoudian (IVPP).

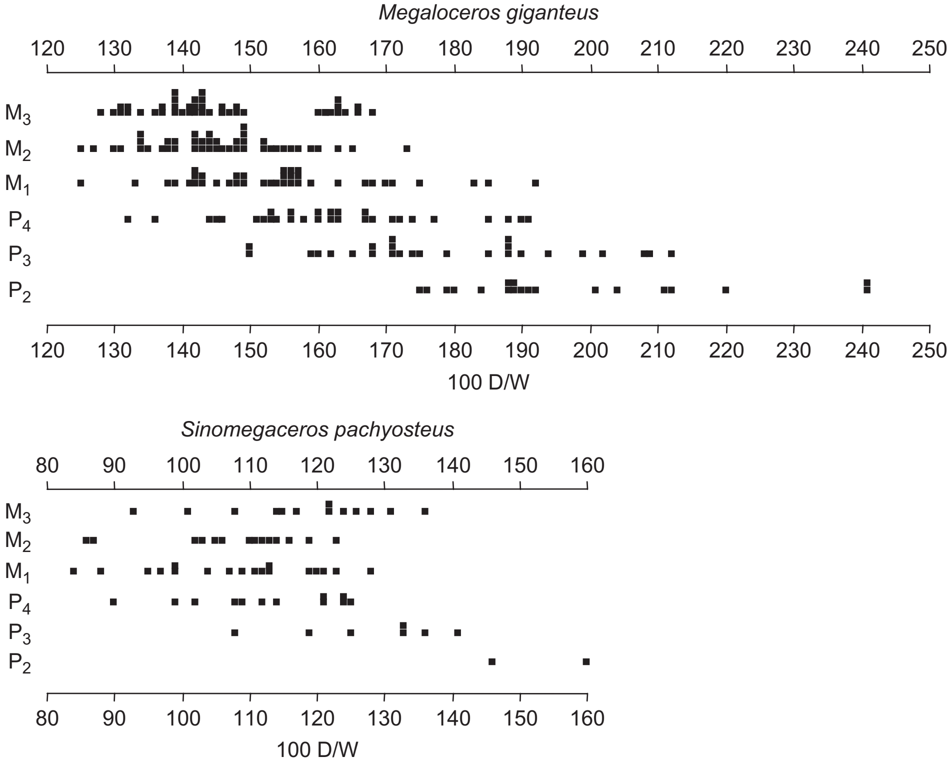


Fig. 15. Variation of the robusticity along the horizontal ramus, as indicated by the index 100 D/W, in *S. pachyosteus* from Zhoukoudian loc. 1 and loc. 13 (ZSM, IVPP, IQW, PIN, NKUA) and *M. giganteus* from the Rheinebene (Rhine valley; NMM).

front (which is more advantageous for a carnivore). In the former case, the power of the temporalis muscle is exerted on the whole tooth row at more or less the same time, whereas in the latter case it is exerted on a section of the tooth row at a time. In the first case, a large amount of not very resistant food can be processed, while in the second case higher pressure can be exerted, especially at the back of the tooth row. Grazing species tend to have the condyle higher than browsers and omnivores. The differences in position of the mandibular condyle form part of the complex interplay of gnathic morphology and the powers exerted by the different muscles that are involved in mastication. Here we define a way to measure the position of the mandibular condyle (section on material and methods; Fig. 5).

The results are presented in Fig. 16. There is a large sample of *M. giganteus* from the Rheinebene, which shows the range of variation that is to be expected. Two lines are indicated in the figure; these represent the proportions height/distance equal to 1/5 and 1/6 respectively. The entire *M. giganteus* sample and two values from the left and right mandibles of one individual of *S. yabei* are above the line with $L/H = 1/5$ and all specimens of *Megaloceros* aff. *savini* from Madrid, and *S. konwanlinensis* and *S. pachyosteus* are below the line $L/H = 1/6$. They are thus well separated.

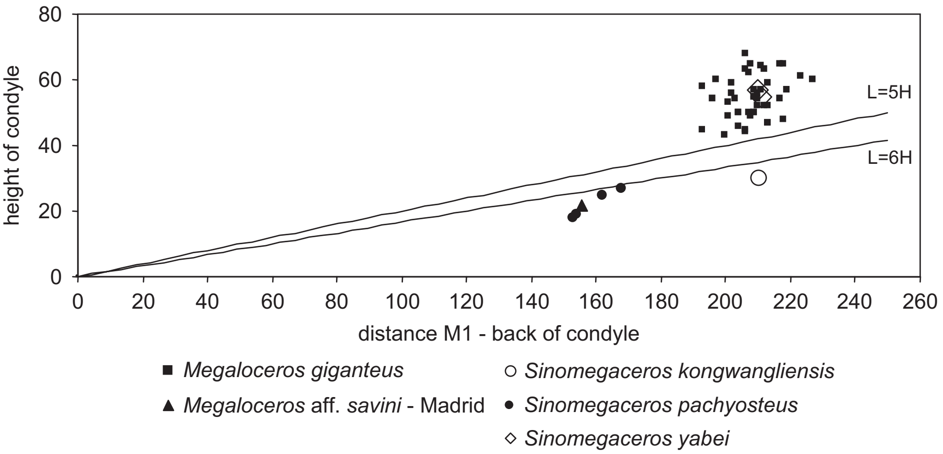


Fig. 16. Position of the mandibular condyle. *S. pachyosteus* from Zhoukoudian (IVPP), *Sinomergaceros konwanlinensis* from Gongwangling (approximate values; IVPP), *S. yabei* from Japan (limestone quarry at Isa town, cast UK), *Megaloceros* aff. *savini* from Transfesa (Madrid; MNCN), *M. giganteus* from the Rheinebene ("Rhine valley", NMM).

M. giganteus and *S. yabei* have the mandibular condyle thus in a position, that is more in accordance with a grazing habit. In the other species, the condyle is lower, which would, in general, suggest a more browsing habit. However, as indicated above, a lower position of the mandibular condyle permits a more gradual closure of the mandible, which allows the forces of the masticatory muscles to exert their force on a more limited section of the tooth row, resulting in a higher pressure.

3.8. Morphology P_4

The degree of "molarisation" of the P_4 is a character that is often used, but also abused (Janis and Lister, 1985); in some species the morphology appears to be more variable than in others and caution is needed in the interpretation. In the different species of ruminants, there is a tendency for the premolars to become more complex and more similar to molars. In the fourth premolar, this process tends to be most advanced. For the Cervidae this process is described and discussed by Heintz (1970). The "molarisation of the premolars" is a process that tends to increase the mastication surface in the anterior part of the tooth row and thus is expected to reflect a minor shift towards a more grazing habit along the cline from browsing to grazing.

According to the stage of molarisation of a particular group of ruminants, the morphologically relevant details differ. Fig. 17 shows two morphotypes of P_4 that occur within the giant deer; one considered in this context as "not molarized" and the other as "molarized". The main difference is that in the "not molarized" P_4, there is a metaconid without metaprecristid, leaving the anterior valley open at the lingual side, while in the "molarized" P_4 there is a metaprecristid, reaching the paraconid and closing the anterior valley or fossid (nomenclature after Van der Made, 1996). A variant on the latter type has the paraconid displaced posteriorly or a little cristid coming out of the paraconid reaching the metaprecristid and thus closing the anterior valley.

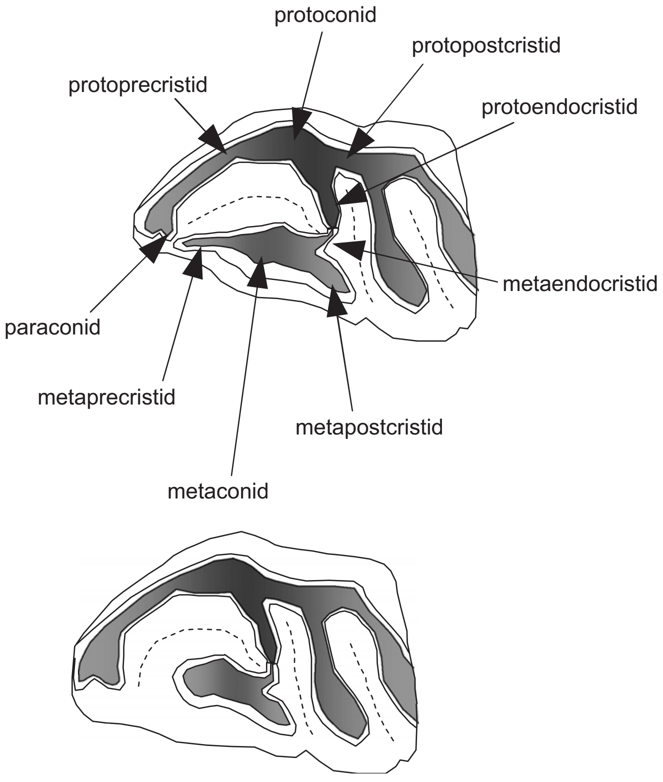


Fig. 17. Two types of P_4, with and without metaprecristid, and the relevant nomenclature of the tooth morphology after van der Made (1996).

The "not molarized" and "molarized" morphologies were checked and were found in the following numbers: *Megaloceros* aff. *savini* from Libakos "not molarized"/ "molarized" = 2/1; *M. savini* from Cúllar de Baza, Pakefield, West Runton and Mundesley 12/0; *Megaloceros* aff. *savini* from Madrid 4/0; *Megaloceros* from Cueva Victoria 1/0; *M. giganteus* from Rheinebene (this sample

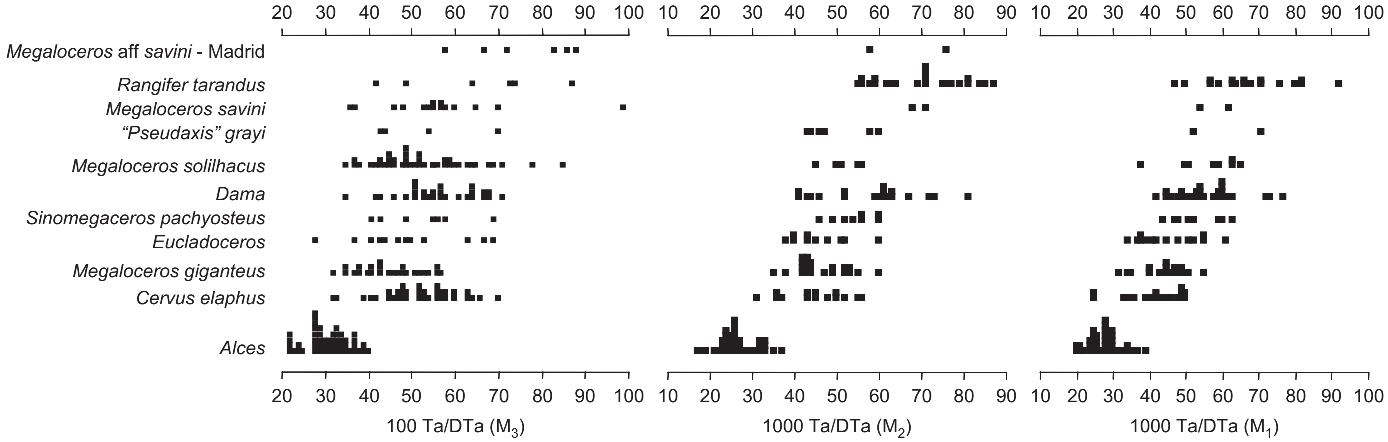


Fig. 18. Enamel thickness in the M_1, M_2 and M_3 of the different species of *Megaloceros* compared to some other Cervidae: *Alces* from Mosbach (NMM), Mauer (SMNK), Voigtstedt (IQW), West Runton (NHM), Süssenborn (IQW), Ehringsdorf (IQW), Rhine valley (NMM), the Netherlands (Dinther, Beegden, un identified locality; NNML), *C. elaphus* from Voigtstedt (IQW), Süssenborn (IQW) and Cueto de la Mina (MNCN), *M. giganteus* from the Rheinebene ("Rhine valley", Eich and Gimbsheim; NMM), *Eucladoceros* from Peyrolles (NHM), Nihowan (MNHN), Olivola (IGF), Valdarno (IGF), and Lachar (MNCN), *S. pachyosteus* from Zhoukoudian localities 1 and 13 (ZSM, IVPP, IQW, PIN, NKUA), *Dama* (incl. "*Pseudodama*") from Olivola (IGF), Il Tasso (IGF), Casa Frata (IGF), Valdarno (IGF), Pyrgos (IVAU), Pinilla del Valle (UCM), recent Spain (MNCN), *Megalcoeros solihacus* from Voigtstedt (IQW), Süssenborn (IQW), Soleilhac (MCP) and West Runton (NHM), "*Pseudaxis*" *grayi* from Zhoukoudian (IVPP), *M. savini* from Pakefield (NHM), Voigtstedt (IQW), Süssenborn (IQW), Cúllar de Baza (MNCN) and Arenero Manuel Soto (Madrid; MSI), recent *Rangifer* (ZMA, NNML) and fossil from Stránská skalá (NMB), Arago (LPT), Eefde (Netherlands, NNML), Wiene (Netherlands, NNML), Bruine Bank (NNML), Ellewoutsdijk (ZMA), St. Michel d'Arudy (IPH), Salp (IPH), Le Placard (IPH), Les Eysies (IPH), and *Megaloceros* aff. *savini* from Madrid (MNCN, MSI, MAN).

0/33), Steinheim, Murr, Ehringsdorf, Schweinskopf, Taubach, the Netherlands (various localities), Ireland 3/60; *S. pachyosteus* 5/11; *S. yabei* 0/3. The general picture is thus that the degree of "molarisation" increased in the geologically younger forms, but that in *M. savini* and *M.* aff. *savini* from Madrid there is no tendency towards molarisation.

3.9. Enamel thickness

Enamel thickness is an interesting feature that is used in the study of many different groups of herbivorous and omnivorous animals, though its use in Artiodactyla is rare. The predominantly omnivorous Suoidea tend to have thick enamel, whereas Suidae that are interpreted to be folivorous tend to have thinner enamel (van der Made, 1996, 2004).

The results presented in Fig. 18 show that there are great differences in enamel thickness between the different species of Cervidae. The species are arranged according to enamel thickness with the thin enamelled *Alces* at one extreme and the thick enamelled *Rangifer* and *Megaloceros* aff. *savini* from Madrid at the other extreme. The differences seem to be clearer in the M_1 and M_2, than in the M_3. Within a large group of species with intermediate enamel thickness, *M. giganteus* has relatively thin enamel, while *S. pachyosteus* has relatively thicker enamel, and *M. savini* still thicker. Few observations on a cast of *S. yabei* suggest that the species had thin enamel.

A large part of the diet of *Alces* consists of aquatic plants (Nowak, 1991), which are soft, while the diet of *Rangifer* includes coarser and harder items. Grazing species in general, tend to have thinner enamel than browsing species. The small differences in enamel thickness of *Cervus* and *Dama* might reflect subtle differences in the composition of the diet. The differences between *M. savini* and *Megaloceros* aff. *savini* from Madrid on the one hand and *M. giganteus* on the other, suggest that these forms were specialized in different ways and thus evolved divergently. The thin enamel of *M. giganteus* suggests, that within a continuum of dietary adaptations, it is slightly more on the side of the grazers, while the other two forms seem to have specialized more on coarser harder food items. This is in accordance with the results obtained on the position of the mandibular condyle.

3.10. Cheek tooth proportions

It is well known that the proportions of the different teeth within a tooth row reflect dietary adaptations, though generally no great effort is made to quantify this. Usually the length of all premolars or of the P3 and P4 are compared to the combined molar length or length of the whole toothrow. However, this does not reflect the different proportions within the premolar and molar rows, which may vary in an important way in relation to diet. Moreover, this method reduces greatly the samples that can be used to the very complete specimens. Cheek tooth proportions have been studied in detail in the Suoidea, which presents an extremely varied group in this respect (e.g. van der Made, 1999a). Grazers, that ingest large amounts of low quality food, tend to have the posterior molars enlarged. In Suoidea, this either occurs through the addition of lobes to the third molars, or simply by enlarging the third molars with respect to the first molars and to some extend also the second molars. In Ruminants, only the latter strategy occurs. In addition, grazers tend to have shorter premolar rows in comparison to browsers. These morphological adaptations are related to the physics of mastication. Molars and premolars have different functions, the molars, which are situated further to the back receive greater forces in mastication and as a result have thicker enamel or higher crowns to resist these forces or a major abrasion.

Fig. 19 compares the length (DAP) and width (DTp in premolars, DTa in molars) of the cheek teeth. The standard is the large sample of *M. giganteus* from Rheinebene. For each tooth the value given corresponds to ln (average sample)-ln (average standard). These are so called ''Simpson diagrams'', which permit comparing proportions or shape. Before interpreting Fig. 19, it should be noted that this figure is based on the averages of samples. The *M. giganteus* sample from Rheinebene is large, while the samples from Ireland and Zhoukoudian are smaller, and the others consist of very few specimens. If there are few specimens, and especially if these include isolated teeth, the proportions may not be representative of the population from which the sample was taken.

Megaloceeros giganteus from Ireland is larger than from Rheinebene, with either a slight relative increase of the posterior molars or slight reduction of the premolars, but over all, similar in proportions to that from Rheinebene. *Sinomegaceros pachyosteus* is slightly smaller, with premolars that seem to be relatively large or wide. *M. savini* is small, especially in the posterior molars. *Megaloceros* aff. *savini* from Madrid is still smaller, with small M_3 and large premolars. Because these observations coincide in the two samples of otherwise very similar *Megaloceros*, it seems that the observations are representative and not an artifact of the small size of the samples. Moreover, large premolars are also found in *E. giulii* and thus an adaptation that is documented also in a larger sample. *Megaloceros* aff. *savini* from Libakos is smaller than the *Megaloceros* from Rheinebene, but does not differ greatly in proportions, save for that the M_1 seems short and wide, but this might due to the inclusion of a well worn specimen. All this suggests, that most of giant deer with palmate brow tines considered here, have tooth rows with more or less the same proportions, but that *M. savini* and *M.* aff. *savini* from Madrid have relatively small M_3 and large premolars.

The small M_3 in *M. savini* and *M.* aff. *savini* from Madrid, compared to the other species, means either, that the tooth was reduced in these two forms, or that it became larger in the other forms. A decrease in M_3 in an artiodactyl is unexpected, since in the well documented cases, the M_3 increased in size or remained stable. The fact, that the earliest European representative of this group has large M_3, is suggestive of a reduction in these two forms, but is not conclusive. However, as we will see in the following section, *M.* aff. *savini* from Madrid has relatively small M_3 for its size as indicated by the limb bones. This suggests, that the small M_3 are the result of reduction.

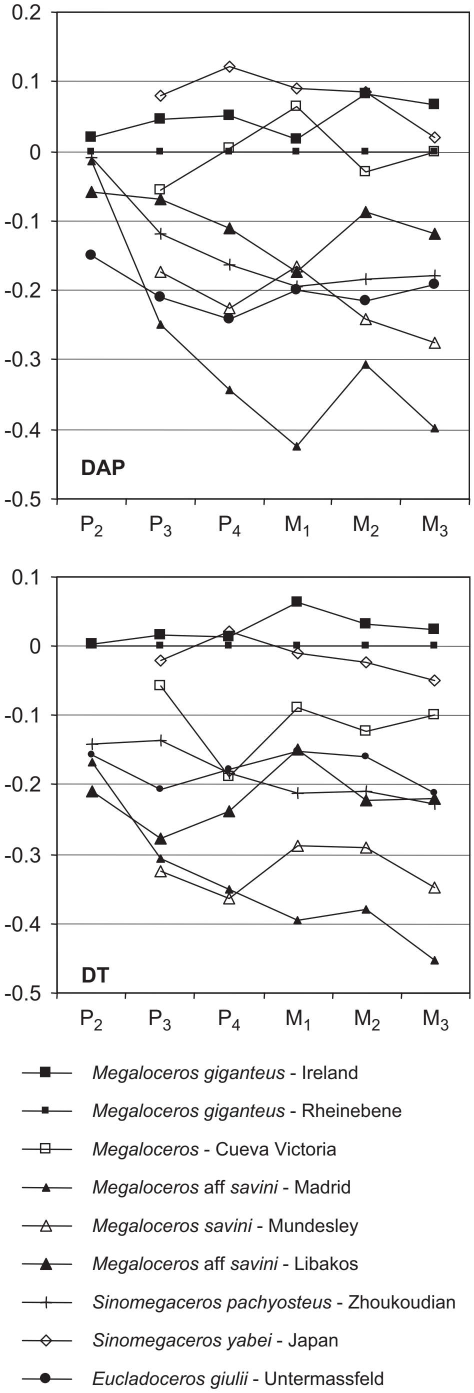


Fig. 19. Proportions of the cheek teeth, the upper graph is based on the DAP of the cheek teeth and the lower on the DTp for the premolars and DTa for the molars. The values are for each tooth ln (average sample)-ln (average standard). Standard is *M. giganteus* from Rheinebene (NMM), in addition: *M. giganteus* from Ireland (NHM), *M. savini* from Mundesley (NHM), *Megaloceros* aff. *savini* from Madrid (MSI, MAN, MNCN) and Libakos (TUC), *Megaloceros* from Cueva Victoria (MAC), *S. pachyosteus* from Zhoukoudian loc. 1 (ZSM, IVPP, IQW, NKUA), *S. yabei* from Japan (limestone quarry at Isa town; cast KU) and *E. giulii* from Untermassfeld (IQW).

3.11. Size

In phylogenetic studies, size is generally given limited importance, though it is a key parameter in palaeoecological and zooarchaeological studies. In those studies, the body weight is used. A variety of methods exist to estimate body weight, using teeth, limb bones, and the skull (e.g. Legendre, 1986; Damuth and MacFadden, 1990; Martinez and Sudre, 1995). Each estimate is a step that decreases precision. Here the width of the first lobe of the M_3 is used as a proxy of body size. Unlike in Suidae, where dietary adaptations are reflected by widely different proportions within the tooth row (e.g. van der Made, 1999b), the differences in the proportions of the cheek teeth in the giant deer, are much more limited, but existing, as we have seen in Section 3.6. Therefore we use a measurement of a post cranial element as a check.

Fig. 20 shows the width of the first lobe of the third lower molar. There is one value for *Megaloceros* aff. *savini* from Libakos, which suggests that the species is on average intermediate in size between *M. savini* and *M. giganteus* and this observation is confirmed by numerous other teeth and bones from the same locality. The values of *M. savini* and *Megaloceros* aff. *savini* from Madrid suggest a gradual size decrease. The smallest values are in the lower range of *C. elaphus* and in the upper range of the largest *Dama*. There is a great jump in sizes to *Megaloceros* aff. *giganteus* and *M. giganteus*, which are large forms. *M. giganteus*

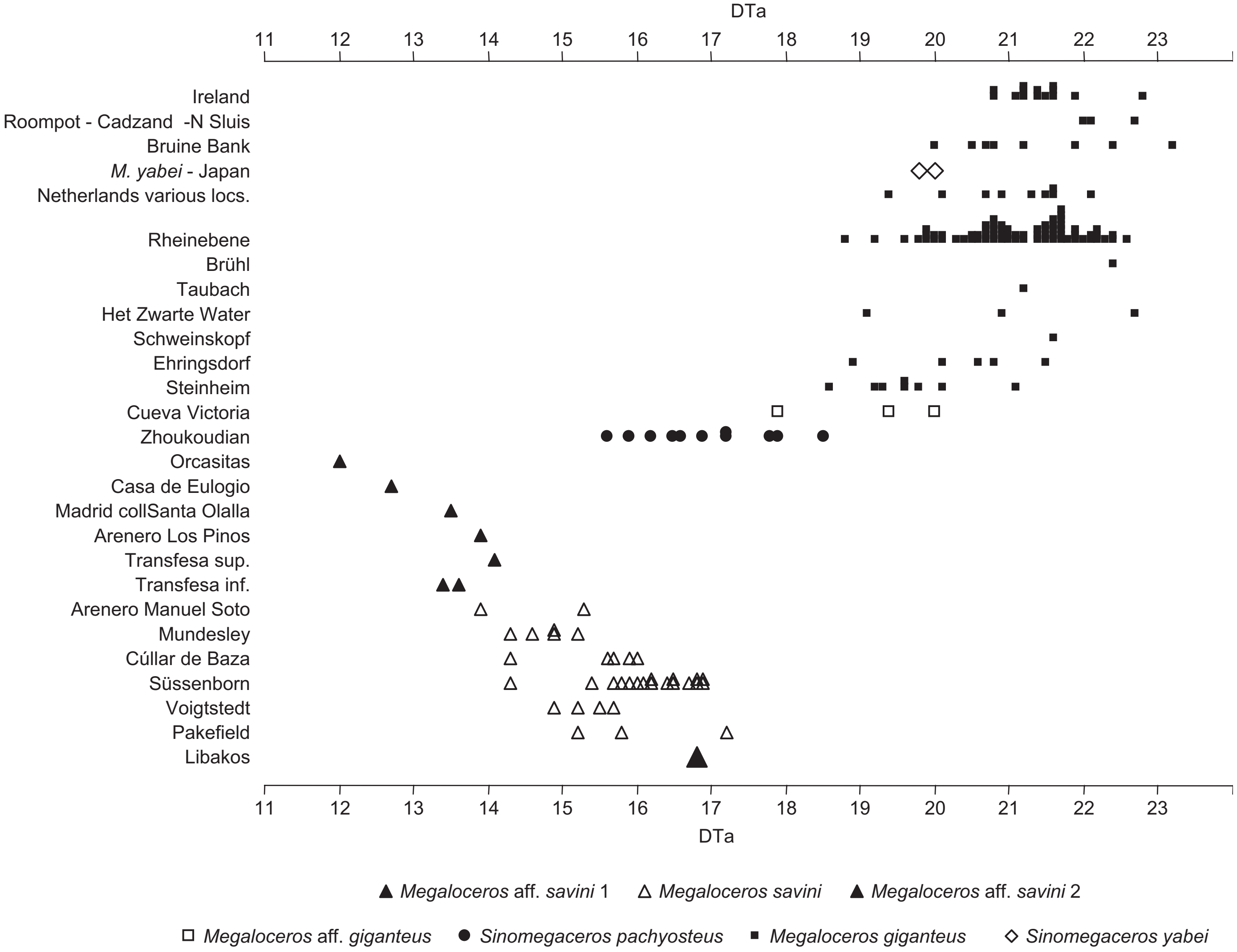


Fig. 20. Size as indicated by the width of the first lobe (DTa) of the third lower molar. The localities are in approximate order from old (bottom) to young (top): Libakos (TUC), Pakefield (NHM), Voigtstedt (IQW), Mundesley (NHM), Süssenborn (IQW), Cúllar de Baza I (MNCN), Tafesa inferior (MAR), Arenero de Manuel Soto (MSI), Arenero Los Pinos (MAN), Transfesa superior (MNCN), Los Pinos (MSI; the specimen is dammaged and the value indicated is a mininmum value), "Madrid" coll. Santa Olalla (MAN), Arenero de Casa de Eulogio), Orcasitas (MSI), Zhoukoudian (mostly loc. 1, representing in reality a long time range; ZSM, IVPP, IQW, NKUA), Cueva Victoria (MAC), Steinheim (SMNS), Ehringsdorf (IQW), Het Zwarte Water (NNML), Taubach (IQW), Brühl (the Rhine valley; SMNS), the Rhine valley (NMM), Netherlands (Ellewoudsdijk, Rossum, Beegden, Zwollekerspel, Hasselt, Mastenbroeker Polder, Koerhuizenbeek, Andel; NNML), Japan (limestone quarry at Isa town; cast in KU), Bruine Bank (North Sea bottom; IVAU), Netherlands (Roompot, Nieuwe Sluis, Cadzand; NNML), Ireland (NHM).

increased a little in average size, but this is a very small increase. No specimen of *S. konwanlinensis* from Gongwangling is included. Other material of this species suggests, that it is of intermediate size, at least as large as the deer from Libakos. *S. pachyosteus* is of intermediate size, larger on average than *M. savini*, but smaller than *M. giganteus*, while *S. yabei* is large, possibly as large as *M. giganteus*.

Though there are less measurements, the distal width of the metacarpal shows broadly the same pattern (Fig. 21). A difference is the very small metacarpal of *S. pachyosteus*. Young (1932) gave measurements of the smallest and largest of a number of specimens. The sole specimen that is included here is close in size to the smallest specimen of Young, which might explain why the teeth indicate an intermediate size and this bone a small size. The M_3 of *M. savini* and *Megaloceros* aff. *savini* from Madrid are small, respectively much smaller than the sole specimen from Libakos, but the metacarpal from Madrid has a similar distal width. Also other bones of the *Megaloceros* from Madrid are relatively large compared to the M_3. These observations suggest, that effectively the M_3 was reduced in these two forms.

3.12. Robusticity metacarpal

The robusticity of the cannon bones is a character that is often studied. Whereas in ungulates, the antero-posterior and transverse diameters of the limb bones tend to be correlated to body size, the correlation of length and body size decreases greatly from humerus/femur to radius/tibia and further to the metapodials (Scott, 1990). Elongation of the metapodials and to a lesser extend the radius and tibia is often taken to reflect cursorial adaptations (e.g. Gambaryan, 1974; Garland and Janis,1993; Köhler, 1993). In bovids, cursorial adaptations tend to be well developed in species that live in open habitats, and, in general the smaller the species, the more elongated the metapodials. This latter observation probably does not reflect allometry, since even the very large giraffes have very elongate metapodials. In stead it may reflect the need for a minimal stride length and speed in small bovids in order to escape predators, while in some occasions groups of large bovids may defend themselves rather than flee. While short or robust metacarpals are primitive, it seems that the fusion of the third and fourth metacarpals is related to the elongation of these elements because: (1) the mechanical necessity to strengthen this section of the hand and foot, (2) the ruminants that reflect this stage of evolution (e.g. passing from *Gelocus* to the earliest Pecora) show a tendency to elongate the metapodials. Therefore, short and robust metapodials seem to be a derived character within the context of the Bovidae and Cervidae. Such metapodials evolved as an adaptation to insular environments (e.g. De Vos, 1979; Matsumoto and Otsuka, 2000; van der Made, 2005a), rocky or mountainous environments (as in Caprinae), semi aquatic habits (as in *Bubalus*), and might have evolved according to Allan's rule (as in *Ovibos*?) or as a result of a different anti predator behaviours (as in *Syncerus* and *Cephalopus*). In Cervidae, the robust metapodials of *Rangifer* might follow Allen's rule.

Fig. 22 is a bivariate plot showing the distal width and length of metacarpals of selected deer. The lines indicate robusticity indices. *Dama* and *Cervus* have relatively slender metacarpals. *Eucladoceros* is not included in this graph, but tends to have metapodials as large as or much larger than the largest *C. elaphus*, with proportions close to L = 6DTd. The small *S. pachyosteus*, *Megaloceros* aff. *savini* from Madrid and slightly larger *Megaloceros* aff.

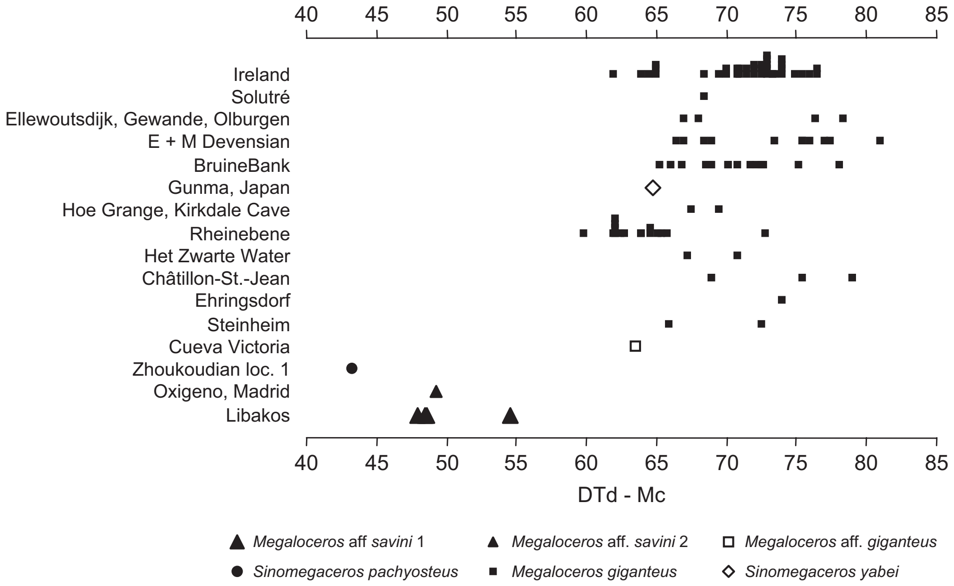


Fig. 21. Size as indicated by the distal width of the metacarpal (Mc). Provenance of data as in Fig. 22; in addition: *Megaloceros* aff. *giganteus* from Cueva Victoria (MAC).

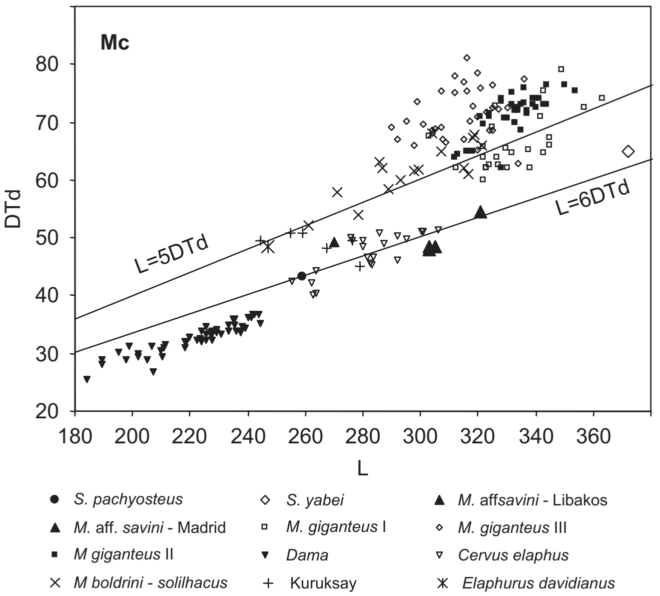


Fig. 22. The metacarpals of the giant deer and selected other species compared (length L versus distal width DTd): *Megaloceros* aff *savini* 2 from Oxigeno (Madrid; MAN); *M. giganteus* I (= *M. g. antecedens-germanicus*) from Steinheim (Lister, 1994), Ehringsdorf (IQW), Het Zwarte Water (NNML), Châtillon-St.-Jean (Lister, 1994), the Rhine valley (NMM), Hoe Grange (Lister, 1994); *M. giganteus* II (= ?*M. g. giganteus*) from Kirkdale Cave, Roc Traucat, Kent's Cavern, Bad Canstatt, Breitenfürter Höhle, Pin Hole, Picken's Hole, Pair-non-Pair, Solutré (all Lister, 1994), Ellewoudsdijk, Gewande, Olbruggen, Bruine Bank (NNML); *M. giganteus* III (= ?*M. g. hiberniae*) from Ireland (NHM), *S. pachyosteus* from Zhoukoudian loc. 1 (ZSM); *S. yabei* from Gunma Prefecture (Japan; Shikama and Tsugawa, 1962); *Megaloceros* aff. *savini* 1 from Libakos (TUC), *Megaloceros boldrini-solilhacus* from Ubeidiya (HUJ), Voigtstedt (IQW), Trimmingham (NHM), Sidestrand (NHM), Mudesley (NHM), Süssenborn (IQW), Soleilhac (MCP), *Dama* (incl. "*Pseudodama*") from Montopoli (IGF), Ubeidiya (HUJ), Tegelen (NMMa), Valdarno (incl. Il Tasso, and Casa Frata; IGF), Petralona (AUT), Neumark Nord (LVH), Lehringen (HMV), Gimbsheim (NMM) and recent *Dama mesopotamica* (HUJ), *C. elaphus* from Voigtstedt (HUJ), Petralona (AUT), Neumark Nord (LVH); recent *Elaphurus davidianus* (NNML) and deer from Kuruksai (PIN). The lines indicate robusticity indices L = 5 DTd and L = 6 DTd.

*savin*i from Libakos are close in size to large *C. elaphus* and have similar robusticity, with proportions close to L = 6DTd. Even the large *S. yabei* has this degree of robusticity. All *M. giganteus* are robust, with values close to, or far superior to L = 5DTd. In this species there are important changes in the robusticity of the metacarpals (Lister, 1994) and possibly the most extreme robusticity evolved only in western Europe (van der Made, 2006).

Megaloceros solilhacus and related forms, are predominantly known from Europe and have robust metacarpals with proportions close to L = 5DTd. The few metacarpals that belong to early representatives of this group, suggest, that these forms aquired and avanced degree of robusticity as early as in Ubeidiya. As is the case in the metacarpals, the first phalanx shows great differences in robusticity, probably reflecting the same adaptations (Fig. 23). It is however, not clear whether increase in robusticity in the phalanges and metapodials follow the same trajectories in the different species. There are several first phalanges from Ubeidiya, which are intemediate in robusticity between those of *C. elaphus* and *E. giulii* on the one hand and *M. giganteus* and *M. solilhacus* on the other, and thus confirm that some degree of robusticity was acquired as long ago as 1.4 Ma (the assumed age of Ubeidiya). Also the phalanges from Libakos show that this *Megaloceros* had aquired some degree of robusticity.

The observation, that robust metacarpals (and phalanges) evoloved in parallel in *M. solilhacus* and *M. giganteus* is of interest. Both are predominantly known from Europe, the first group from about 1.4–0.3 Ma and the second group from about 0.5–0.01 Ma. In addition, within *M. giganteus*, robusticity increased further in western Europe ("*M. giganteus* III in Fig. 22), but probably not as much in eastern Europe or western Asia (van der Made, 2006). This suggests, that during more than a million years, different giant cervids forms adapted in a similar way to the environment of western Eurasia. In eastern Eurasia these adaptations did not evolve in the giant deer. This might reflect a fundamental difference between the western and eastern Eurasian environments. However, robust metacarpals occur in *Elaphurus* (Fig. 22), a deer that is smaller than any of the giant deer with robust metacarpals. This raises the question whether the east Asian giant deer did not evolve robust metacarpals because of *Elaphurus*, or whether the environment was fundamentally different in east and west Eurasia.

4. Discussion

In order to answer the question, whether dispersals of giant deer with palmate brow tines between east and west Eurasia may have occurred, we reconstructed the phylogeny of these deer in a way, which we believe to reflect parsimoniously the results obtained in the previous chapter (Fig. 24). It is given in the form of a tree with branches that may consist of anagenetic lineages, and not in the form of a cladogram. If taking temporal distribution into account, a tree with anagenetic lineages may be more parsimonious and informative than a wildly branching cladogram, that is limited to morphological data and that by default shows each predefined entity as if it were a separate lineage. The numbers in Fig. 24 refer to the characters or changes that are discussed below.

(1) Most giant deer in this analysis, including the earliest species, share: a palmate brow tine, that is inclined medially, a high separation of brow tine and main beam, at least moderately robust mandibles, a mandibular condyle in low position, enamel thickness as in most cervids, relatively large M_3 and relatively small premolars, and a size that is intermediate considering the size ranges of the giant deer. The palmate brow tine is the character that defines Azzaroli's, 1953 "*M. giganteus* group". Palmate brow tines are not found in any other group of cervids, and thus might be an interesting synapomorphy. However,

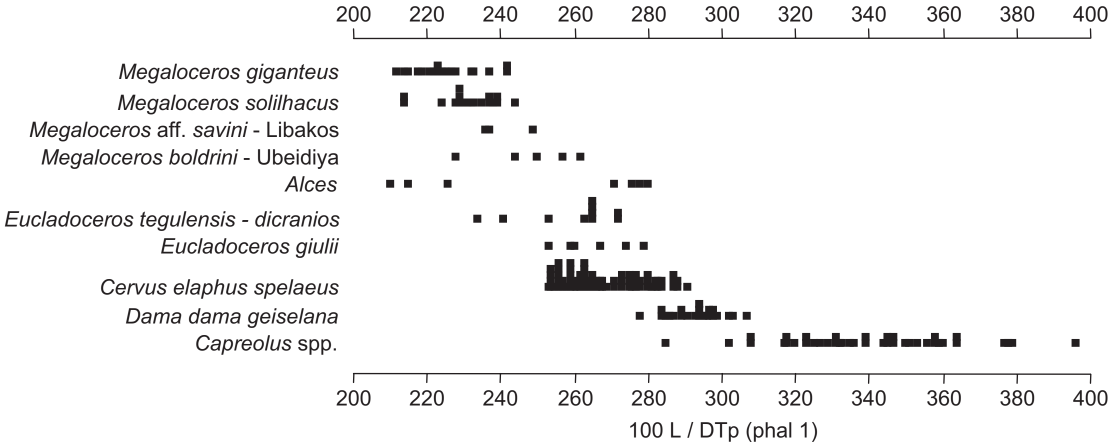


Fig. 23. The robusticity of the first phalanx, as indicated by index 100 L/DTp, compared: *M. giganteus* from Ireland (NHM), *M. solilhacus* from Voigtstedt (IQW), Süssenborn (IQW), Soleilhac (MCP) and West Runton (NHM), *Megaloceros* aff. *savini* from Libakos (TUC), *Megaloceros boldrini* from Ubeidiya (HUJ), *Alces* from East Runton (NHM), Voigtstedt (IQW), Süssenborn (IQW) and Mauer (SMNK), *Eucladoceros tegulensis-dicranios* from Tegelen (NHMMa) and Il Tasso (IGF), *C. elaphus spealeus* from Neumark Nord (LVH), *D. dama geiselana* from Neumark Nord (LVH), and *Capreolus* from Voigtstedt (IQW), Süssenborn (IQW), Koneprusy (NMP), Miesenheim (FASMN), Azykh V (MUB), Grotte des Cèdres (MRA), Ehringsdorf (IQW), Can Rubau (CIAG) and Cueva Morín (MNCN).

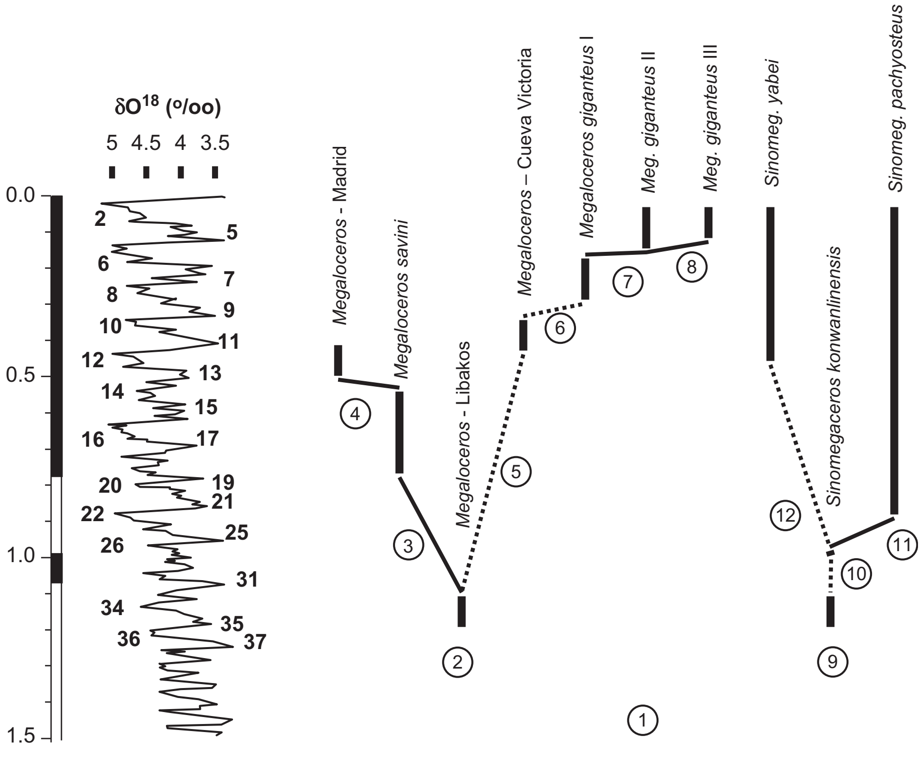


Fig. 24. The proposed phylogenetic relationships and temporal distributions of the giant deer with palmate brow tines. The thick lines indicate temporal distribution, thin lines probable relationships, stippled lines possible relationships. The numbers indicate changes or characters that are discussed in the text.

various forms with bifurcating brow tines, like *Arvernoceros* and *Elaphurus*, might have given rise to deer with palmate brow tines. To know whether palmate brow tines appeared only once or various times, ancestral forms should be studied. Pachyostosis or robust mandibles are found in a wide variety of cervids and apparently evolved several times in parallel, which makes it suspicious as a plesiomorphy for this group. Moreover, there are differences in the degree of robustness along the mandible. The enamel thickness is probably primitive, that is, with intermediate values.

(2) Presence of a "second tine" and probably of a third tine, both arising from the anterior side of the main beam and directed anteriorly; P_4 variable with both "not molarized" and "molarized" morphotypes.

(3) Lowering of the bifurcation of main beam and brow tine, size decrease, reduction of the size of the third molar, apparent increase in size of the premolars, possibly thicker enamel and possibly reduction of degree of "molarisation" of the P_4.

(4) Further size decrease, thicker enamel, and larger premolars, possibly further lowering of the bifurcation of brow tine and main beam.

(5) Size increase, lowering of the bifurcation of the brow tine and main beam, palmation brow tine dipping laterally in at least part of the specimens, presence/absence of distal palmation unknown, degree of robusticity of metapodials unknown, position manidbular condyle unkown.

(6) Distal palmation originating from branched "third tine", lowering of the bifurcation of separation of brow tine and main beam, palmation brow tine dips laterally in all adults, mandibular condyle in high position, predominantly "molarized" P_4, robust metacarpals, and large body size.

(7) Slight increase in robusticity of the metacarpals.

(8) Further increase in robusticity of the metacarpals.

(9) Lack of a second tine, long anteriorly curved main beam without "second tine" and with palmation at the end, and as a continuation of, the main beam; degree of "molarisation" of the P_4 not known.

(10) Palmation brow tine transversely oriented; P_4 variably molarized.

(11) Important increase in pachyostosis, main beam becoming shorter, resulting in distal palmation moving proximally, size decrease.

(12) Size increase, mandibular condyle in higher position, thinner enamel; P_4 probably predominantly molarized.

In this model the characters listed under 2 and 9 are given much weight: the presence of a "second tine" and presumed structure that gave rise to the palmation. The "third tine", which in *M. savini* bifurcated various times, originates at the anterior side of the main beam and gave rise to a bifurcation in *M. giganteus*. In this sense, it is treated as an important synplesiomorphy of *M. savini* and *M. giganteus*. Contrary to this, the palmation of *Sinomegaceros* is situated at the end of a long main beam without "second tine" and forms a continuation of the main beam. Though superficially both groups of giant deer are similar in having some kind of a palmation, the detailed morphology of these palmations, and probably also their origin, is different. In addition to the differences in the morphology of the distal palmation, its appearance at very different times in both groups, is suggestive of the distal palmation appearing twice. Whereas there are important differences between *Megaloceros* ans *Sinomegaceros*, there are striking similarities in the same characters between *S. konwanlinensis* and *A. ardei*, which share the long curved main beam and the shape of the distal palmation. The appearance of an occasional bifurcation in the brow tine of *Arvernoceros* (Heintz, 1970, Figs. 295, 296, 301, 302, 302, 306, 313, 315) is suggestive of the origin of a palmate brow tine, which would make the similarity very great indeed. If these morphological similarites between *A. ardei* and *S. konwanlinensis* are no mere parallelisms, the former species might be more related to the latter, rather than to the European *M. giganteus* and *M. savini* (as was supposed by Vislobokova, 1990). Such a relationship would imply that a distal palmation evolved convergently in *M. giganteus*, which is not contradicted by the facts of an absence of a palmation in *M. savini* and the late appearance of this structure in *M. giganteus*. Similarly such a relationship casts doubt on the palmate brow tine being a character that unites *Sinomegaceros* and *Megaloceros*.

If the model presented in Fig. 24 is correct, dispersals between east and west Eurasia did not play a part in the phylogeny of these deer. Also the appearance of elevated mandibular condyles, thinner enamel, "molarized" P_4 and larger body size in *M. giganteus* and *S. yabei* are parallellisms. The characters in question are known to have evolved in several groups in parallel or convergently. "Molarized" P_4 were acquired parallel in *Cervus*, *Dama* and in Odocoilinae (*Capreolus*, *Rangifer*, *Alces*), and a large number of other ruminants. Thinner enamel evolved independently in *Alces*, *Cervus* and even in the suid *Listriodon*. Moreover, if species of *Megaloceros* and *Sinomegaceros* changed to a more grazing habit in conjunction with size increase, all these changes may have been correlated. The increase in robusticity of the mandible seems to have proceeded parallel culminating in west Eurasia in *M. giganteus* and in east Eurasia in *S. pachyosteus*. The latter species reached a much higher degree of robusticity than the west Eurasian species, and did so at an earlier geological age.

Alternatively, these characters are no parallellisms but are synplesiomorphies of *S. yabei* and *M. giganteus*, and consequently the former species should be placed in *Megaloceros*. The palmation in *Arvernoceros* may end in three tines, which seems to be taken by Heintz (1970, Figs., 295, 296, 315) as the fully adult morphology. The posterior one of these tines, superficially resembles a small tine in *S. yabei*. However, the resemblance between this tine in *S. yabei* and the "back tine", that is found in young *M. giganteus* and in *D. dama* and which has been commented on above in chapter 3, Section 3.5, is much greater. If this resemblance is more than superficial, the origin of the palmation might be identical in both species, which then might be closely related. If that would be the case, *M. yabei*, must have lost its second tine and must have acquired a transversely and upward directed brow tine in parallel to *S. pachyosteus*. It is obvious, that here we have problems to separate synapomorphies from parallelisms and that further work is necessary. In any case, the mandibular and dental characters are interesting for various reasons, even if their value in the reconstruction of the phylogeny is not quite clear.

S. tadzhikistanis was supposed to be ancestral to the other species of *Sinomegaceros* (Vislobokova, 1990), including the species discussed above. Vislobokova (1988) described from Kuruksai three new species and two more possible species: *Axis flerovi*, *Elaphurus eleonorae*, *Elaphurus* sp., *S. tadzhikistanis* and *Eucladoceros* sp. Earlier, Sharapov (1986) had described already *Elaphurus palmiroalajensis* from Kuruksai. The cervid metapodials from Kuruksai are indicated in Fig. 22 and fall apart in two groups: some specimens are long and elongate and are close to line $L = 6DTd$, while others are shorter and wider and are close to line $L = 5DTd$. The more robust metapodials have proportions that are similar to those of recent *Elaphurus*. The more slender specimens from Kuruksai, are similar in size and proportions to *C. elaphus*, and thus similar in these respects to *Eucladoceros* and much larger than those of recent *Axis* and *Pseudaxis grayi* from Zhoukoudian (not in Fig. 22). The teeth come in two size classes and do not show spectacular differences in morphology. The antlers are mainly represented by basal fragments. There are two morphologies. The specimens assigned to *Elaphurus* and *Sinomegaceros* have a high bifurcation and a very large brow tine, that may be slightly flattened or bifurcated, but not clearly palmate. They have a long main beam, that at some distance of the base curves anteriorly and that at the end may become slightly flattened. The specimen assigned to *Axis* has a lower bifurcation and a round brow tine that curves upward. The specimens assigned to *Eucladoceros* are similar, but larger and tend to have a wider angle between brow tine and main beam. The two latter types might as well represent antlers of juvenile and fully adult individuals. In short, there is evidence for an *Elaphurus* species and another species, which might be close to *Axis* or *Eucladoceros*, but with metacarpal robusticity closer to that of *Eucladoceros*. Though some species of *Elaphurus*, that retained relatively gracile metapodials, might have been ancestral to *S. pachyosteus*, there is no convincing evidence, that the forms present in Kuruksai represent such an ancestral form.

Data on enamel thickness, the position of the mandibular condyle, tooth proportions and probably also the degree of "molarisation" of the P_4, reflect different methods of food processing. Three different combinations are recognized: (1) intermediate enamel thickness, low mandibular condyle, large M_3 and relatively small premolars with a variable degree of "molarisation"; (2) thick enamel, low mandibular condyle, small M_3 and relatively large premolars that are predominantly "not molarised"; (3) relatively thin enamel, elevated mandibular condyle, large M_3 and relatively small premolars that are predominantly "molarized". The first combination seems to be primitive and is found in *Megaloceros* aff. *savini* from Libakos, *S. konwanlinensis*, and *S. pachyosteus*. Each one of the other two combinations seem to be a complex of adaptations to a different feeding strategy. The third combination is a set of characters that is generally found in animals that are more or less adapted, but not extremely adapted, to grazing, and is here found in *M. giganteus* and *S. yabei*. The second combination of characters seems to be an adaptation to hard and coarse food, that needs to be masticated with great pressures. It is found in *M. savini* and *Megaloceros* aff. *savini* from Madrid.

Though there are many exceptions to this tendency, in general, large ruminants tend to be grazers and small ruminants tend to be browsers. This trend is well described for bovids (Estes, 1974; Jarman, 1974). Small bovids are capable to select parts of particular plants, while large mammals eat greater quantities and are much less selective. Small bovids tend to live in smaller social units in closed environment and be territorial all year round. Large bovids tend to live in large social units, in open environments, are not territorial and migrate during the year in accordance with optimal food availability. Between these extremes there is a continuum. Horn size and morphology changes along with social structure: horn cores are small and simple in species that live in the smallest social units, largest and most spectacular in the largest bovids that are still territorial, while in species that live in very large mixed herds, also females tend to have horns. In this sense, masticatory adaptations towards more grazing in parallel with size increase in *M. giganteus* and *S. yabei* are not unexpected. Similarly a size decrease in *M. savini*—*M.* aff. *savini* from Madrid is consistent with masticatory adaptations towards a more specilized or browsing feeding habit. If we extrapolate the social structure of the bovids to these giant deer, we would expect that these large deer lived in larger social units and may have been migratory. The appearance of larger and more conspicious antlers would fit this pattern. This certainly is the case with the appearance of palmation in *M. giganteus*, but the antlers of *S. yabei* are small for the size of this huge deer.

Given the areas and environments in which the fossils of the giant deer were found, an increase in metapodial robustness of the species studied here might reflect Allen's rule and be an adaptation to cold climate or might be the result of a different social structure and anti predator behaviour. Small bovids (and other similar sized herbivores) live in closed environments and the principal anti predator behaviour is sprint and hide. These bovids have short and robust metacarpals and tend to have smaller fore limbs than hind limbs, resulting in high back quarters and a back that slopes down anteriorly. Bovids of intermediate size live in larger groups in more open environments and tend to escape by fleeing; they are not sprinters but stayers, and have long metapodials and fore and hind limbs of similar length. Large bovids tend to live in larger herds and often adopt the strategy of defending themselves. Well known is the behaviour of musk oxen to stand in a circular formation with the heads and horns directed outward. This conduct is not restricted to these bovids, but occurs in other species as well. Aggressive behaviour of *Syncerus* is well known (Leuthold, 1977). Bovids may defend themselves against a small predator and flee from a larger predator. Bovids with defence strategies (rather than fleeing) tend to have shorter metapodials. The more robust metapodials in the giant deer are found in *M. giganteus* and the *M. solilhacus*-lineage. These are truly large deer. The idea that they may have defended themselves from relatively large carnivores is tempting and would fit other characteristics such as a shift towards more grazing, large antlers and large body size, which parallel characteristics of bovids that live in larger social units and that may defend themselves from predators. However, it is difficult to see how such a hypothesis could be tested. Because the robust metapodials appeared several times in the west but not in the east Eurasian giant deer, it seems likely, that this character has something to do with a feature of the west Eurasian environment, that was not present in the east.

5. Conclusions

(1) A phylogenetic model of the evolution of *Megaloceros* and *Sinomegaceros* is presented (Fig. 24).

(2) The model is in accordance with the two genera being separate, rather than a single genus, because the distal palmations are different in morphology and origin and originated at different times and thus probably evolved convergently. *Megaloceros* has a second tine and a third tine, that is bifurcated again, or that gave rise to a palmation, while *Sinomegaceros* has no "second tine" and the palmation is a distal contiunation of the main beam. *Sinomegaceros* acquired a distal palmation by the late Early Pleistocene, whereas *Megaloceros* acquired it in the second half of the Middle Pleistocene.

(3) There is no evidence of dispersals between west and eastern Eurasia after the oldest samples studied here (Gongwangling and Libakos), though there is a considerable amount of parallel or convergent evolution in these genera, involving lowering of the first bifurcation, appearance of distal palmation,and possibly, the palmate brow tine in the antlers and pachyostosis in the mandibles.

(4) Several characters suggest that *M. savini* and related forms adapted to a diet that includes coarser and harder food. These characters include: thicker molar enamel, reduced posterior molars and larger premolars, and a P_4 with a lesser degree of "molarisation".

(5) *M. giganteus* aquired a set of characters that suggest that it adapted to grazing larger quantities of not very hard food. These characters include: an elevated mandibular condyle, thin enamel, and a P_4 that is predominantly "molarized".

(6) Since the masticatory adaptations in *M. giganteus* are divergent from those of the *M. savini*-lineage, the latter does not seem to be ancestral to the former species, which may have arrived in western Europe by dispersal.

(7) *M. giganteus* is unique among the giant deer with palmate brow tines in having very robust metapodials. This character evolved several times in western Eurasia: during the Early Pleistocene in the *M. solilhacus* group (with round brow tines), not later than the late Middle Pleistocene in *M. giganteus* and it increased in the Late Pleistocene *M. giganteus*. Since the character did not evolve in the east Eurasian giant deer, the character might be related to some aspect of the west Eurasian environment that was not present in east Eurasia.

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