

## The evolution and biogeography of the Pleistocene giant deer *Megaloceros giganteus* (Cervidae, Mammalia)

With 10 figs, 1 tab., 1 pl.

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### Abstract

The giant deer *Megaloceros giganteus* is one of the emblematic Pleistocene mammals. Material from various Dutch localities and large samples from Germany and the North Sea were studied and compared with data and results of studies by LISTER (1994) and STUART et al. (2004) and a hypothesis on the evolution and biogeography of the species is proposed. The earliest representatives of this species had relatively long and slender limb bones. During the Eemian, a sudden and important increase in robusticity occurred in the west European populations, while in the east European populations, robusticity increased only a little. The robust branch became extinct around 20 ka ago (uncalibrated radio carbon years). Between 10 to 13 ka, western Europe was colonized from eastern Europe by *Megaloceros* with limb bones of an intermediate robusticity. These changes in the robusticity of the limb bones are mainly caused by changes in length of the bones and seem to be related to locomotion, while body weight seems to have changed little.

**Key words:** Cervidae, *Megaloceros*, evolution, biogeography, stratigraphy, Pleistocene

### Introduction

The giant deer *Megaloceros giganteus* is an emblematic Pleistocene species, which lived across a large area from Europe to east of Lake Baikal (R.-D. KAHLKE 1999). As many other species, it became extinct at the end of that epoch. This extinction turns out to have been a more complex event than previously believed. STUART et al. (2004) have shown that *Megaloceros* went extinct in western Europe around 20 ka ago, but that it reappeared between about 13 to 10 ka (uncalibrated radiocarbon yr). The genus survived in the intermediate period in the area north of the Black and Caspian seas, from where it might have re-colonized western Europe. This scenario is contrasted here with earlier observations by LISTER (1994) on *Megaloceros giganteus*, who noted that: “The limb proportions in the earliest and latest samples are ‘normal’, but in an intermediate episode (Ipswichian and Early-Middle Devensian) the animals generally had short distal elements”. He concluded that no model clearly accounts for the differences in body size and proportions, but thought it to be “the result of a complex interaction between population division, adaptation, ecophenotypic response and change factors”. Some aspects of the metacarpals, dentition and antlers from samples from

the Rhine valley, the North Sea and the Netherlands will be discussed and compared with samples described by LISTER (1994). A hypothesis on the evolution and biogeography of *Megaloceros* is proposed.

### Material and methods

The specimens published by LISTER (1994) are compared with material from several Dutch and German localities (see next section), which is largely unpublished. The material is kept in institutes, which are indicated with the following abbreviations:

FWUB	Institut für Paläontologie der Rheinischen Friedrich-Wilhelms Universität Bonn.
IGF	Istituto di Geologia, now Museo di Storia Naturale, sez. Geologia e Paleontologia, Firenze.
IQW	Forschungsstation für Quartärpaläontologie, Weimar (Forschungsinstitut Senckenberg).
LVH	Landesmuseum für Vorgeschichte, Halle.
MNCN	Museo Nacional de Ciencias Naturales, Madrid.

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NHM Natural History Museum, London.  
 NMM Naturhistorisches Museum, Mainz.  
 NNML Nationaal Natuurhistorisch Museum, Leiden.  
 SMN Forschungsbereich Altsteinzeit Schloss Monrepos, Neuwied (Römisch-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte).  
 SMNS Staatliches Museum für Naturkunde, Stuttgart.

Although most of this material has not been published in detail, detailed descriptions are available of material from Steinheim (BERCKHEMER 1941), Mundesley (AZZAROLI 1953), Süssenborn (H.-D. KAHLKE 1967), Ehringsdorf (H.-D. KAHLKE 1968), Taubach (H.-D. KAHLKE 1977), Cúllar de Baza (AZANZA & MORALES 1989) and Neumark Nord (VAN DER MADE 2004).

The sizes and proportions of the metacarpals, antlers and teeth are discussed here. The measurements were taken as indicated by VAN DER MADE (1989, 1999a, 1999b). All the measurements are given in mm and are indicated with the following abbreviations:

DAPb = anteroposterior diameter of the antler, measured just above the burr.  
 DAPm = minimal anteroposterior diameter of the shaft of the cannon bone.  
 DAPp = proximal anteroposterior diameter of the cannon bone.  
 DAPpf = anteroposterior diameter of the proximal articular surface of the cannon bone.  
 DAP III = anteroposterior diameter of the distal articulation of Mc III.

DAP IV = anteroposterior diameter of the distal articulation of Mc IV.  
 DTa = transverse diameter or width of the anterior lobe of the  $M_3$ .  
 DTd = distal width of the cannon bone.  
 DTm = minimal width of the cannon bone.  
 DTp = width of the proximal articulation of Mc IV.  
 DTPf = width of the distal articulation of Mc IV.  
 DT III = width of the distal articulation of Mc IV.  
 DT IV = width of the distal articulation of Mc IV.  
 Hext = distance from below the burr to the bifurcation of the brow tine and main beam, measured on the lateral (external) side.  
 L = length of the metacarpal.  
 L3 = an alternative measurement of the length, measured as the "I" of the Mc III (VAN DER MADE 1996).  
 L4 = an alternative measurement of the length, measured as the "I" of the Mc IV (VAN DER MADE 1996).

### Localities

*Megaloceros giganteus* was nearly absent from a major study of fossil deer from the Netherlands (KUNST 1937) and most remains were collected much later on and are unpublished. Most of the localities where these fossils come from have not been published either, and therefore a small introduction is given here, as well as to the localities of the Rhine valley in Germany.

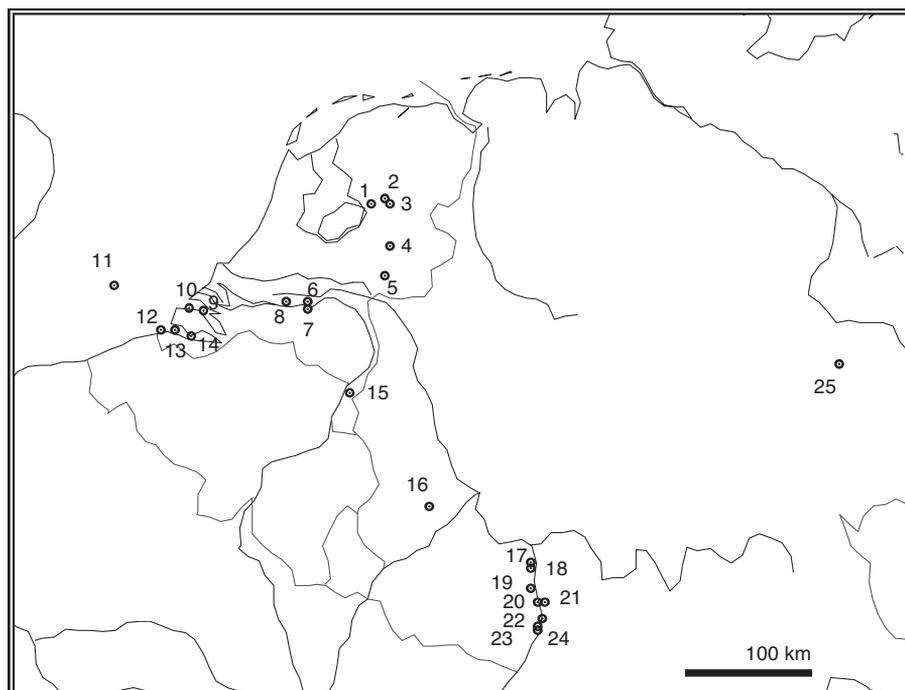


Fig. 1: The geographical position of the Dutch and German *Megaloceros* localities mentioned in this study, but not mentioned by LISTER (1994): 1) Mastenbroeker Polder; 2) Het Zwarte Water and Hasselt; 3) Zwollerkerspel, 4) Koehuizenbeek, 5) Olburgen; 6) Rossum; 7) Gewande; 8) Andel; 9) Colijnsplaat, 10) Roompot, 11) Bruine Bank, 12) Cadzand off-shore; 13) Nieuwesluis; 14) Ellewoutsdijk; 15) Beegden; 16) Schweinskopf, 17) Gimbsheim; 18) Eich; 19) Lampertsheim; 20) Altrip; 21) Edingen; 22) Brühl, 23) Otterstadt; 24) Rheinhausen; 25) Neumark Nord.

Bruine Bank (Brown Bank) (fig. 1). Huge collections of fossils have been made from the bottom of the North Sea by fishermen using beam trawls to catch flatfish. These nets pass through the upper few centimetres of the sea bottom dragging up fossils of large mammals in a large area of the North Sea between the Netherlands and England. The journal 'Cranium', published by the Werkgroep Pleistocene Zoogdieren, regularly contains papers on these fossils. General information on the North Sea fossils is given by DREES (1986), BOSSCHA ERDBRINK (1993a, b) and VAN KOLFSCHOTEN & LABAN (1995). The conditions of collecting are fairly well known, and nowadays the coordinates of the fossil finds tend to be known. There is evidence that the North Sea material represents broadly four different ages according to the areas where the fossils were collected (fig. 2). The Bruine Bank Fm is generally considered to be of late Eemian and early Weichselian age (eg. VAN KOLFSCHOTEN & LABAN 1995), though a specimen was radiocarbon dated around 28 ka (REUMER et al. 2003). Both "glacial" and "interglacial" taxa are collected from this formation. As we will see below, the *Megaloceros* sample from the Bruine Bank has a large variation in robusticity, which might be due to the collection consisting of two subsamples of different robusticity and belonging to two different faunal associations of different ages. If this is the case, the variation in age of the remains still seems to be small and the Bruine Bank Fm seems to cover exactly the time-interval of morphological change in *Megaloceros* metacarpals. The Eem Fm occurs largely in the same areas as the Bruine Bank Fm, but is mainly of marine origin and thus unlikely to yield extensive collections of remains of land mammals.

Many of the Dutch localities are places where sand and gravel are extracted by suction under water. The level reached by the suction pipe determines the maximum age of the fossils, but specimens from higher levels may be admixed. Since the subsoil of most of the Netherlands consists of flat lying sediments, the geological situation tends to be relatively simple (DE MULDER et al. 2003) and stratigraphic control is relatively good, given the way of collecting. Most of the localities in east of the country (fig. 1, nos. 1–8) are in an area, where the fluvial Kreftenye Fm is wide spread. This formation is said to be of Late Saalian to Holocene age. In some places it is overlain by the thin Echteld Fm of Holocene age. Of a much more restricted distribution is the Drenthe Fm, which should be of Saalian age. Most probably, the finds derive from the Kreftenheye Fm. *Ovibos* and *Mammuthus primigenius* have been reported from Rossum (KORTENBOUT VAN DER SLUIJS 1957) and *Coelodonta antiquitatis* and *Bison priscus* from Gewande (GUÉRIN 1980; pers. obs.).

Another group of localities is in the area of the Scheldt (fig. 1; nos. 9–10 and 12–14). The sediments present are assumed to be either of Eemian or younger age, or belong to the Tegelen Formation and other Pliocene to Oligocene formations (DREES 1986). Fossil collecting in the East Scheldt is much in the same fashion as from the North Sea

and remains are either of Late Pliocene–Early Pleistocene, Eemian, Weichselian or Holocene age (KORTENBOUT VAN DER SLUIJS 1985). At Ellewoutsdijk (or Ellewoudsdijk) in the West Scheldt, remains were dredged up that were assigned to *Ovibos* (BOSSCHA ERDBRINK 1983, KERKHOFF & MOL 1991).

Beegden is in an area where the Beegden and Boxtel Formations are wide spread. The fluvial Beegden Fm is Plio–Holocene and the overlying Boxtel Fm is late Middle Pleistocene to Holocene in age.

The sediments of the Rhine in Germany (Rheinschotter) or of the Rhine valley (Rheinebene) are exploited for sand and gravel in the same way as described above for some Dutch localities. These localities and fossils have been studied much more extensively than the Dutch localities. Here material is used that is kept in the Naturhistorisches Museum in Mainz, which comes from the area of Gimbsheim and Eich and material from the Staatliches Museum für Naturkunde in Stuttgart, which comes from localities more upstream like Altrip, Brühl, Edingen, Lampertsheim, Otterstadt and Rheinhausen. Other institutes, like the university in Bonn, have material from still other localities. General information is given by KOENIGSWALD (1988) and a faunal list is given by KOENIGSWALD & HEINRICH (1999). The exact stratigraphic provenance of the material is not known, and the authors considered it a mixture of Eemian and Weichselian elements, and were of the opinion that *Megaloceros* might be of either age. KOENIGSWALD (1988) believed that *Megaloceros* is not restricted to glacial, nor to interglacial environments. FRENZEN & SPEYER (1928) described *Megaloceros* from the Rhine sediments, focusing on cranial material.

A specimen from Schweinskopf is included here, which was described by TURNER (1990, 1991), who also gave an introduction to the locality.

## Results

In a study of *Megaloceros giganteus*, LISTER (1994) noted differences in robusticity in the limb bones, in particular in the metacarpal, metatarsal and radius. Of these bones, the metacarpal is the one that is best represented in the collections and which, in general, shows best the differences in robusticity. Figure 3 includes nearly 60 metacarpals and is based entirely on data provided by LISTER (1994), and shows three groups of metacarpals: slender metacarpals with ages indicated as Holsteinian/Hoxnian, Saalian/Wolstonian or Stage 7 (Stage 7 is Oxygen Isotope Stage or OIS 7, now Marine Isotope Stage or MIS 7); robust metacarpals with ages indicated as Eemian/Ipswichian and Early and Middle Devensian/Weichselian; metacarpals with an intermediate degree of robusticity with an age indicated as Late Devensian. LISTER (1994) noted already that the changes in robusticity are not clearly related to environmental temperature, nor that any other existing model clearly explained these changes.

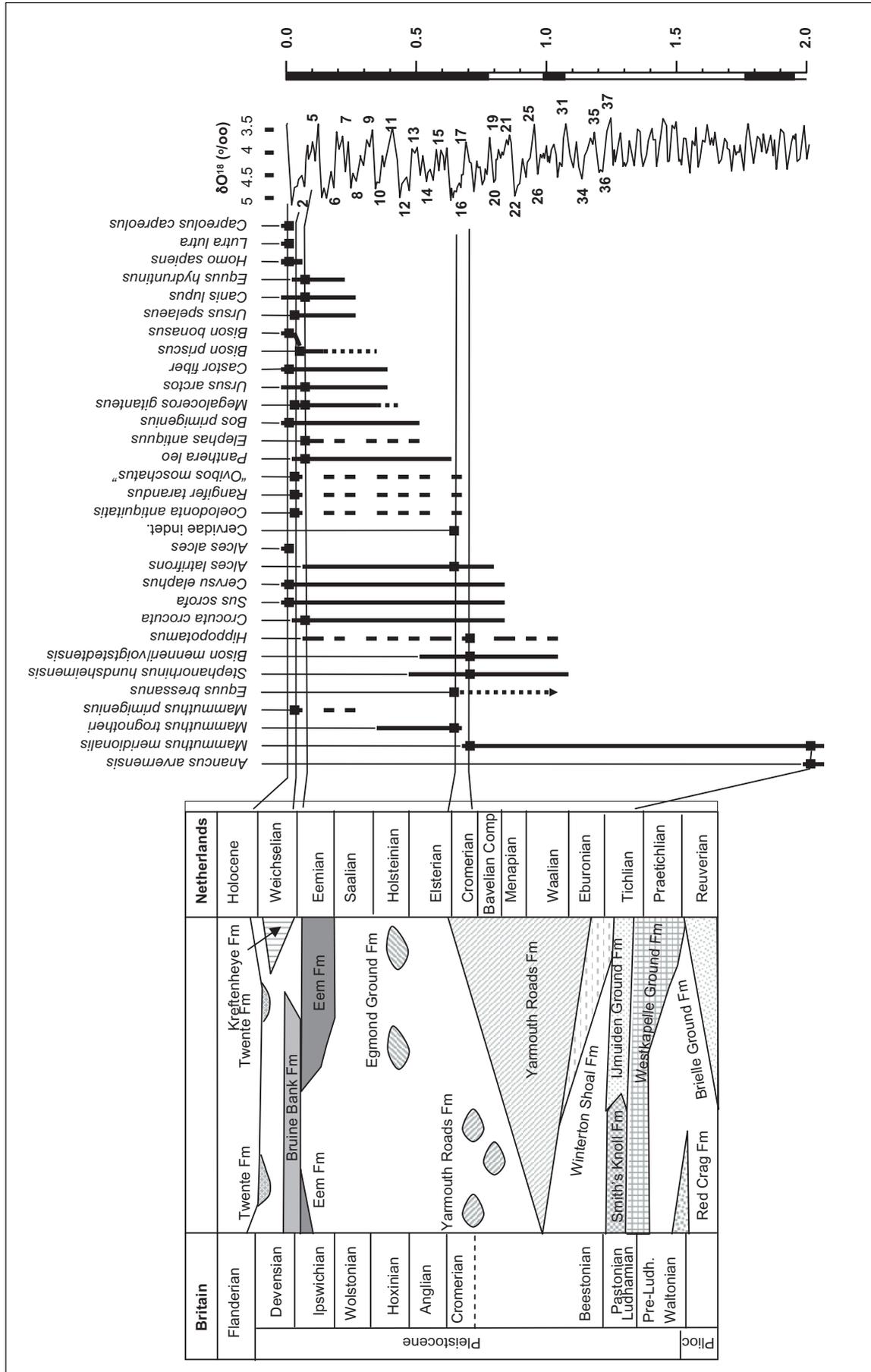


Fig. 2. Sedimentary formations in the North Sea subsoil and the approximate provenance of the mammal associations recovered from the North Sea bottom (after VAN KOLFSCHOTEN & LABAN 1995, but with some changes in taxonomy). Note that the blank parts of the figure are hiatus. There are four broad faunal associations, but some of them appear to represent more than one point in time. These associations are compared to the temporal distribution of these taxa at these latitudes (roughly after VAN DER MADE 2005).

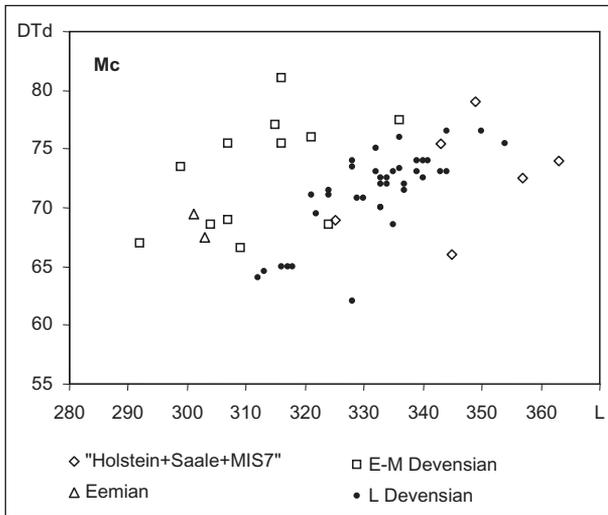


Fig. 3: Bivariate diagram of the metacarpal (Mc) of *Megaloceros giganteus*, distal width (DTd) against length (L): “Holstein + Saale + MIS 7” includes Steinheim, Ehringsdorf and Châtillon-St.-Jean; “Eemian” includes Hoe Grange and Kirkdale Cave; “E-M Devensian” includes Roc Traucat, Kent’s Cavern, Bad Cannstadt, Bereitenfürther Höhle, Pin Hole, Picken’s Hole, Pairnon-Pair and Solutré; L Devensian includes various localities from Ireland. Data and ages according to LISTER (1994).

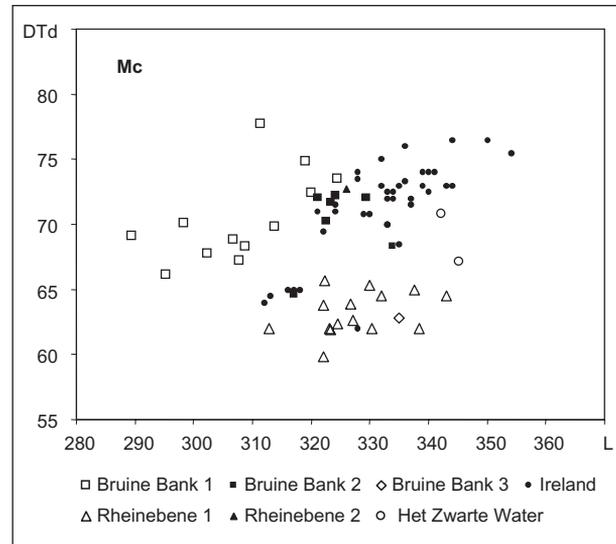


Fig. 4: Bivariate diagram of the metacarpal (Mc) of *Megaloceros giganteus*, distal width (DTd) against length (L): Bruine Bank (n = 19; NNML), Ireland (n = 38; LISTER 1994), Rheinebene (n = 16; NMM), Het Zwarte Water (NNML).

The largest sample of metacarpals is the one from the Late Devensian of Ireland and includes nearly 40 specimens. The sizes are not evenly distributed: there is a large cluster of large specimens and a small cluster of smaller specimens. PFEIFFER (1999) indicated sexually bimodal distributions in metacarpals and other bones of *Dama*. It is not clear whether this apparent bimodal distribution in the Irish *Megaloceros* metacarpals corresponds to a large number of males and a small number of females. However, if an allometric relation is estimated on the basis of this sample, this possible unequal distribution should be taken into account.

The sample from the Rhine valley includes over 20 metacarpals mostly from Eich and Gimbsheim. Most of them form a compact cluster (Rheinebene 1 in fig. 4), with only one specimen being much wider and thus much more robust (Rheinebene 2). The bulk of the sample forms a cluster that is situated to the right of the group of possible female metacarpals from Ireland, but are on average more elongate, while the “Eemian” specimens of LISTER are situated to the left and are thus more robust and cluster with the Early and Middle Devensian specimens of LISTER (fig. 3).

The “Holstein + Saale + MIS 7” group plots to the right of the possible male metacarpals from Ireland. This group contains specimens from Steinheim, Ehringsdorf and Châtillon-St.-Jean and clusters also with specimens from Het Zwarte Water (fig. 5; pl. 1, fig. 3). The question arises, whether the “Holstein + Saale + MIS 7” group could consist mainly of males, and the Rhine Valley sample mainly of females. Since most or all of these specimens

were not found in anatomical connection with a skull (which might reveal the sex by the presence or absence of antlers), this question cannot be answered. Whatever the answer, it should be noted that the variation in the Rhine Valley sample (Rheinebene 1) is very low in comparison to the other samples (“Ireland”, E-M Devensian, Bruine Bank, etc.).

The specimens from the Eemian/Ipswichian of Hoe Grange and Kirkdale Cave cluster with the Early and Middle Devensian specimens (fig. 5). Specimens from Ellewoutsdijk, Gewande (pl. 1, fig. 2) and Olburgen in the Netherlands are robust like those from the Early and Middle Devensian studied by LISTER (1994) (fig. 5).

A large sample of some 20 specimen from the Bruine Bank (Brown Bank) is not homogenous in its proportions (fig. 4; tab. 1). One specimen (no. 139583, informally indicated as Bruine Bank 3) is long and relatively gracile and is well separate from the other specimens from the Bruine Bank, yet it plots in the middle of the sample from the Rhine valley. It is also close to the metapodials of *Megaloceros solilhacus* (not indicated in fig. 2), which is known from the early Middle Pleistocene. There are three possible explanations: 1) this specimen is the oldest one from the Bruine Bank and is early or middle Eemian in age, 2) the specimen is not from the Bruine Bank but from the Egmond Ground Formation and belongs to very early *M. giganteus*, 3) the specimen is still older and comes from the Yarmouth Roads Fm. and belongs to *M. solilhacus*. This specimen is not further considered here. The remaining specimens from the Bruine Bank form one cluster. However, most of the specimens (indicated as Bruine Bank 1)

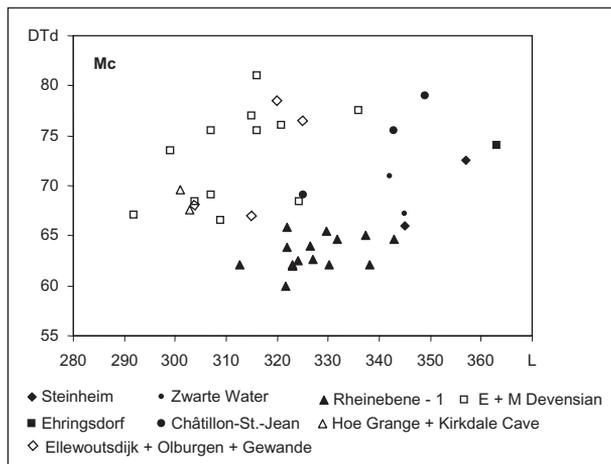


Fig. 5: Bivariate diagram of the metacarpal (Mc) of *Megaloceros giganteus*, distal width (DTd) against length (L): Steinheim, Ehringsdorf, Châtillon-St.-Jean, Hoe Grange, Kirkdale Cave and various localities of Early and Middle Devensian age (Roc Traucat, Kent's Cavern, Bad Cannstadt, Breitenfürther Höhle, Pin Hole, Picken's Hole, Pair-non-Pair, Solutré) (LISTER 1994), Rheinebene (NMM), Het Zwarte Water (NNML) and Ellewoutsdijk, Olburgen and Gewande (NNML).

plot to the left of the sample from Ireland, roughly where LISTER's (1994) Early and Middle Devensian specimens do (fig. 3), while some of the specimens (indicated as Bruine Bank 2; pl. 1, fig. 1) fall within the ranges of this sample. This might be explained in two ways: 1) the more slender specimens are from the time interval when robusticity increased, 2) they are not from the Bruine Bank Fm, but from the Twente Fm (and thus be approximately co-eval with the Irish sample). Of some specimens the provenance is indicated in the collection as "Bruine Bank?" (see tab. 1), but both are robust. Therefore the first explanation seems to be the most likely.

Figure 6, in which all metapodials are represented, shows three distinct groups: slender, robust and intermediate. These groups include the material described by LISTER (1994) and the newly described material, which increases the sample size for the two earlier morphotypes from some 20 to 60 specimens. The groups have the respective tentative age ranges: Holstein to (Early?) Eemian, (Middle and Late ?) Eemian to Middle Weichselian and Late Weichselian. The increased samples confirm the presence of three types (gracile, robust and intermediate), which had been observed already in fig. 3. The Eemian samples either group with the robust (Kirkdale Cave, Hoe Grange) or with the gracile morphotypes. Each of the three morphotypes or groups seems to fall apart into a group of larger and a group of smaller specimens (fig. 6). This reinforces the possibility of a marked sexual bimodality in limb bone size. However, as said before, this needs further study.

The length, distal width and a robusticity index of the metacarpals are indicated in fig. 7. The localities or groups of localities are arranged according to approximate age. The Rhine Valley and Bruine Bank sample are treated

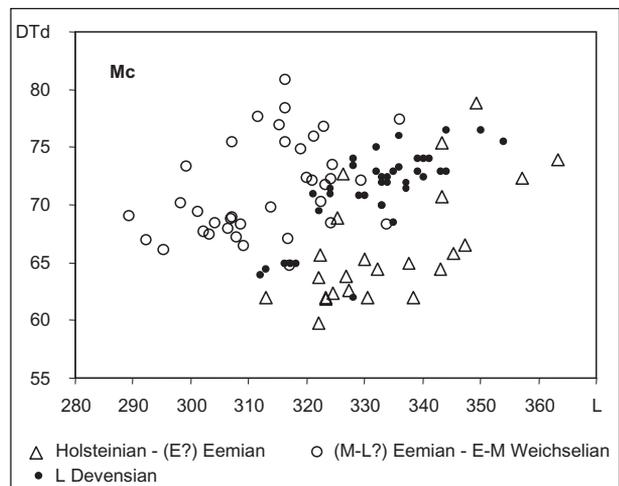


Fig. 6: Bivariate diagram of the metacarpal (Mc) of *Megaloceros giganteus*, distal width (DTd) against length (L). Provenance of data: Zwarte Water, Bruine Bank, Ellewoutsdijk, Gewande and Olburgen (NNML) and Rheinebene (NMM) and data from LISTER (1994). The localities are grouped in three groups, slender, robust and intermediate, corresponding to the following ages (largely following LISTER 1994): Holstein - (E?) Eemian/Ipswichian includes Steinheim, Ehringsdorf, Châtillon-St.-Jean, Het Zwarte Water and Rheinebene; (M-L?) Eemian/Ipswichian - E-M Weichselian/Devensian includes: Hoe Grange, Kirkdale Cave, Roc Traucat, Kent's Cavern, Bad Cannstadt, Breitenfürther Höhle, Pin Hole, Picken's Hole, Pair-non-Pair, Solutré, Ellewoutsdijk, Gewande, Olburgen, and Bruine Bank; and L Weichselian/Devensian includes Ireland.

here as single samples. It is apparent that in any level or sample, there is a wide variation in distal width, save if the sample is very small. Again, the relatively large Rhine Valley sample is very compact with one outlier. The length shows a clear decrease from Steinheim to Bruine Bank and Solutré, after which there is a break and again relatively great length in the sample from Ireland. If the samples from Steinheim to Châtillon-St.-Jean represent mainly males and the sample from the Rhine Valley mainly females, this apparent gradual decrease in size in these samples might not be real; the decrease from these samples to Hoe Grange, Kirkdale and the Early and Middle Devensian samples seems to be real. The robusticity index shows relatively low values (implying relatively gracile metapodials) in the samples from Steinheim to the Rhine Valley. Hoe Grange and Kirkdale Cave and later samples are more robust. Again there is a rupture, when robusticity decreases in the sample from Ireland.

Some independent characters were studied to see whether they give additional information. One of these is the variation through time in the sizes of the cheek teeth. Here the variation of the width of the third lower molar ( $M_3$ ) is given, one of the most commonly found elements (fig. 8). A comparison is also made with *Megaloceros savini*, a species that is closely related (R.-D. KAHLKE 1999, VAN DER MADE 2001, 2004). Whereas *Megaloceros gigan-*

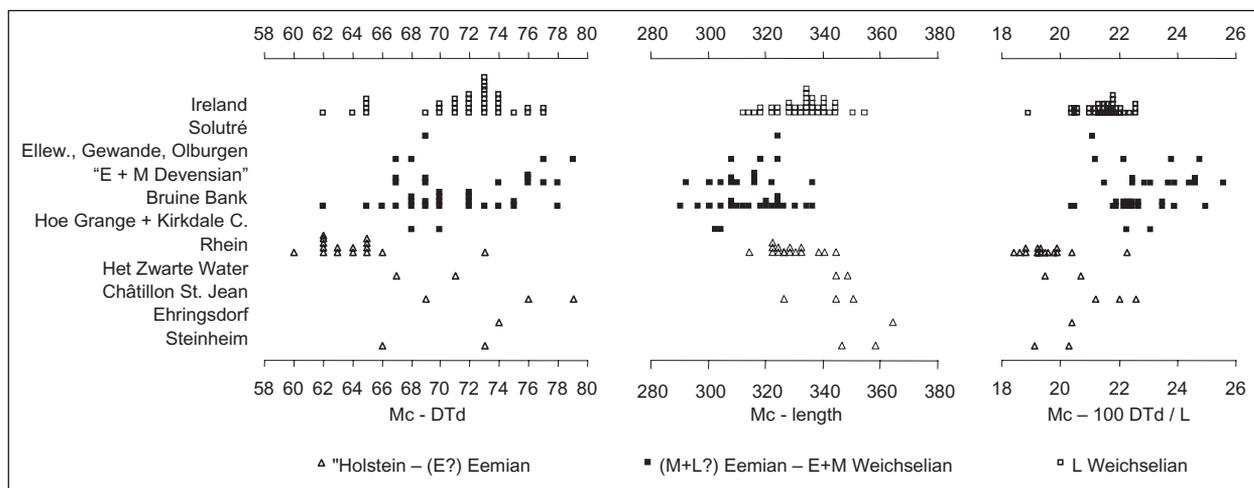


Fig. 7: Distal width (DTd), Length (L) and robusticity (100 DTd / L) in the metacarpal of *Megaloceros giganteus*. The localities are arranged in approximate order from old (bottom) to young (top). Provenance of material as indicated in figures 3–6.

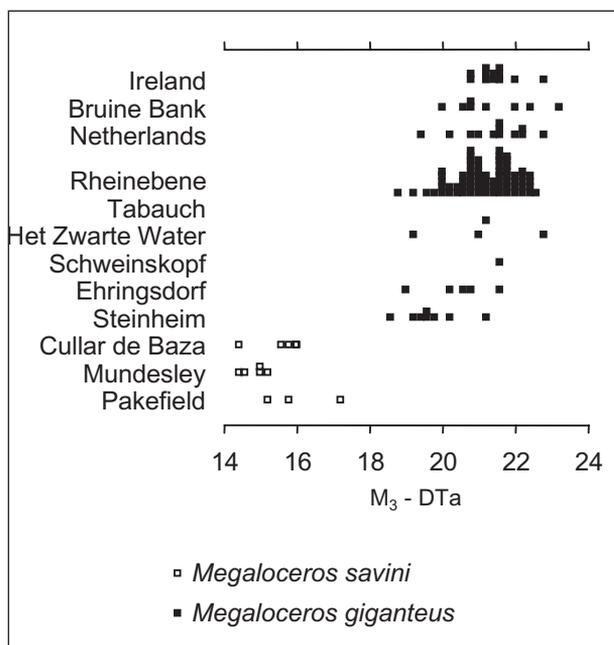


Fig. 8: Width of the anterior lobe (DTa) of the  $M_3$  in *Megaloceros*. The localities are arranged in approximate order from old (bottom) to young (top): Pakefield (NHM), Mundesley (NHM), Cúllar de Baza (MNCN), Steinheim (n = 8; SMNS), Ehringsdorf (IQW), Het Zwarte Water (NNML), Schweinskopf (SMN), Taubach (FWUB), Rhein (Eich, Gimbsheim, etc.; n = 70; NMM), Netherlands (Ellewoutsdijk, Rossum, Beegden, Zwollerkerpel, Hasselt, Mastenbroeker polder, Koehuizenbeek, Andel, Roompot, Nieuwe Sluis – Wester Schelde –, Cadzand off shore; n = 12; NMML), Bruine Bank (n = 8; NMML), Ireland (n = 12; NHM).

*teus* and *Megaloceros savini* differ clearly in size, there is no evidence for important differences in size between the different *M. giganteus* samples, at least as evidenced by the size of the third lower molar. There seems to be a more or less bimodal size distribution in the large sample from the Rhine Valley. This is suggestive of a sexual bimodality,

which contrasts with the metapodials, which, save for one specimen, form a compact cluster (fig. 4).

*Megaloceros giganteus* differs from the older and more primitive *Megaloceros savini* in that the bifurcation of the brow tine and main beam is situated closer to the burr. There is, however, no evidence for further change in the position of the bifurcation in the subsequent samples of *M. giganteus* (fig. 9).

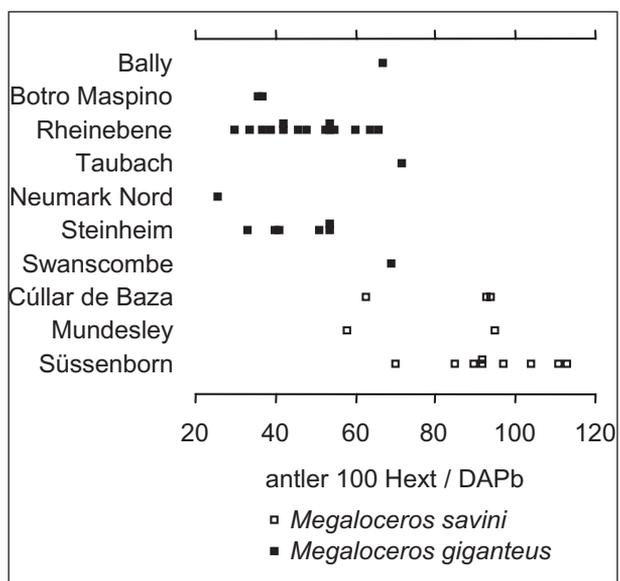


Fig. 9: Index 100 Hext / DAPb in the antler. (Hext = distance from below the burr till the bifurcation between brow tine and main beam, measured at the lateral side; DAPb = antero-posterior diameter, measured just above the burr; measurements as indicated by VAN DER MADE 1999a, b) The localities are arranged in approximate order from old (bottom) to young (top): Süssenborn (n = 10; IQW), Mundesley (NHM), Cúllar de Baza (MNCN), Swanscombe (NHM), Steinheim (n = 6; SMNS), Neumark Nord (LVH), Taubach (IQW), Rhein (Altrip, Brühl, Otterstadt, Lampertsheim, Rheinhausen, Edingen; n = 15; SMNS), Botro Maspino (IGF), Bally (Ireland; NNML).

## Discussion

The new samples that are included here tend to confirm the earlier observation by LISTER (1994) that the earlier *Megaloceros* have long and relatively elongate limb bones, that later robusticity increased, while the youngest *Megaloceros* is again relatively slender (figs. 6 and 7). Though classification of these samples is not the primary aim of this paper, the theme has to be commented on.

The three different types are currently all included in a single species *Megaloceros giganteus* (LISTER 1994), though AZZAROLI (1953) preferred to raise *M. antecedens* to species rank. Previous authors proposed a variety of species or subspecies names, which are currently all included in *M. giganteus*. ROGER (1887) listed the following forms: *Cervus (Dama) euryceros* ALDROVANDI, *Cervus megaceros* HART, *Cervus irlandicus* BLUMENBACH, *Cervus platyceros altissimus* MOLIGN., *Cervus hibernus* DESMAREST, and *Megaceros hibernicus* OWEN. POHLIG (1892) recognized three species: *Cervus (Euryceros) hiberniae* OWEN (or “*hibernicus*”), *Cervus (Euryceros) germaniae* POHLIG, and *Cervus (Euryceros) italiae* POHLIG.

The publications that treat the taxonomy of *Megaloceros giganteus* do not indicate or discuss the type material, type locality and its possible age, and frequently the original publication of the species by BLUMENBACH is not even cited. I myself have not been able to trace the original publication and do not know the type material (whether it includes limb bones or not), nor its age.

It will not be easy to retrace all type material, though it seems likely that “*irlandicus*”, “*hibernus*” and “*hibernicus/hiberniae*” are based on the Irish material of the Late Devensian with metapodials of an intermediate degree of robusticity.

Various names might apply to the form with the slender metapodials. BERCKHEMER (1941) based *Megaloceros giganteus antecedens* on material from Steinheim, and considered the morphology of the brow tine, the width of the antlers and the short length of the (upper) cheek teeth important characters for the recognition of this taxon, as well as some details of tooth morphology. There is no indication that there are great differences in proportions of the tooth row, and thus the size of the  $M_3$  might be taken as a general indication of size. Fig. 8 compares a great number of cheek teeth and shows a general increase in size. Indeed, the Steinheim teeth are small, but the differences are not spectacular. The antlers are narrow; they are curved backwards and upwards, and not outward as in most *Megaloceros*, including another specimen from Steinheim, which is supposed to be slightly younger (geological age), and the *Megaloceros* in Bonn, which is a type of *M. germaniae*. Though the extent of variation of antler morphology in the earlier populations is not well known, the differences in antler morphology indicated by BERCKHEMER (1941) seem to make sense, since the Steinheim antlers are intermediate between other, more primitive forms of *Megaloceros* (such as *M. savini*) and the

more “typical” or well known later forms of *M. giganteus*. The Steinheim collection includes slender limb bones and thus this name is available for the early slender morph, though this metapodial morphotype might occur with different antler types. One of the specimens on which POHLIG based *M. germaniae* is kept in Bonn and is from the Rhine Valley. It is a skull with wide antlers. It is however, not clear what kind of metapodials it had, though, bearing its provenance in mind, it is possible that they were of the relatively slender type. H.-D. KAHLKE (1968) assigned material from Ehringsdorf to *Megaloceros giganteus germaniae* and described a long and slender metapodial. This opinion is in line with an application of the name “*germaniae*” to *Megaloceros* with slender limb bones. The use of the younger name “*antecedens*” depends thus on whether one accepts the existence of a different taxon, mainly on the basis of antler morphology.

Even though this overview leaves us without knowing which names to apply to the different morphotypes, it should be noted that the number of metacarpals assignable to the slender and robust forms has tripled and the number of localities where they are known is increased. Though some of the samples or localities have their problems, this increase in numbers, implies that the range of morphological variation and the temporal distribution are better known. In the future, the species might become more interesting for biostratigraphy.

As mentioned in the introduction, the Rhine Valley fossils are assumed to be of Eemian to Weichselian age. The observation that the sample from the Rhine Valley has very little metrical variation (save for one outlier) suggests that the sample has very little temporal variation. In addition, it is known that early and middle Weichselian and some Eemian specimens are robust. This suggests that the specimens from the Rhine Valley have more affinity with the earlier slender *Megaloceros*. If the Rhine Valley metacarpals are considered to represent smaller individuals (mainly females?), but otherwise comparable to those of the “Holstein + Saale + MIS 7” group, *Megaloceros* with relatively elongate or slender metapodials must have occurred in western Europe from the Holsteinian till the Eemian.

The Hoe Grange and Kirkdale Cave specimens are Ipswichian/Eemian and are robust; the increase in robusticity must have occurred within the Eemian. Probably the relatively more gracile specimens in the Bruine Bank sample (Bruine Bank 2 in fig. 4) are of Eemian age, and probably close to those from Hoe Grange and Kirkdale Cave. The present data suggest a relatively long period when *Megaloceros* had elongate limb bones, a change from gracile to robust in a short period during the Eemian, again followed by a period of stasis. This might have occurred in two ways: 1) by dispersal of a robust form from outside the study area, 2) by local evolution. In a scenario with the dispersal of a more robust form, no or few intermediate specimens would be found. However, the sample from the Bruine Bank includes several specimens with a degree

of robusticity that is intermediate between the earliest forms and the early and middle Devensian/Weichselian forms (marked Bruine Bank 2 in fig. 4), suggesting local evolution. Also the larger specimen from the Rhine Valley (Rheinebene 2) is not only larger, but also more robust and is close to these specimens from the Bruine Bank. It might be close in age to these specimens and be younger in age than the rest of the sample from the Rhine Valley.

The decrease in robusticity during the latest Pleistocene seems to correspond to the local extinction of *Megaloceros* in western Europe around 20 ka and the new immigration around 13 ka described by STUART et al. (2004). As noted by LISTER (1994), a specimen from Solutré is relatively gracile, but it is not beyond the limits of the increased late Pleistocene robust sample.

Comparing the different diagrams (figs. 3–7), it appears that the variation in robusticity is mainly caused by changes in length of the metapodials, whereas the distal width is more constant. Distal width is more related to body size and length of the metapodials is probably more related to locomotion. This would imply that the observed changes in the metapodials do not so much reflect changes in body size, but rather changes in locomotion. This is supported by the sizes of the cheek teeth, which do not show important differences independently of the length and robusticity of the metapodials in the same samples.

The following hypothesis explains the observations on morphology by LISTER (1994), which are confirmed in the

present study, and the observations on the distribution of *Megaloceros* by STUART et al. (2004). From the Holsteinian till the early Eemian, a *Megaloceros* with relatively slender metapodials had a wide distribution over most of Europe. During the Eemian, this population split up into two subgroups, of which the western European one acquired much more robust limb bones, while an eastern European population became only slightly more robust. This probably reflects different adaptations that affect locomotion, which suggests that the separate populations lived in different environments. Around 20 ka BP, the robust western European population went extinct and around 13 ka the more slender eastern European population dispersed into western Europe. This hypothesis is represented in fig. 10, using some of the available names, though as stated above, more work on the taxonomy of this group is needed.

This hypothesis is testable by studying the morphology of samples from eastern Europe of Early and Middle Devensian/Weichselian ages, by the dating of more samples, and by analysis of DNA of the fossils.

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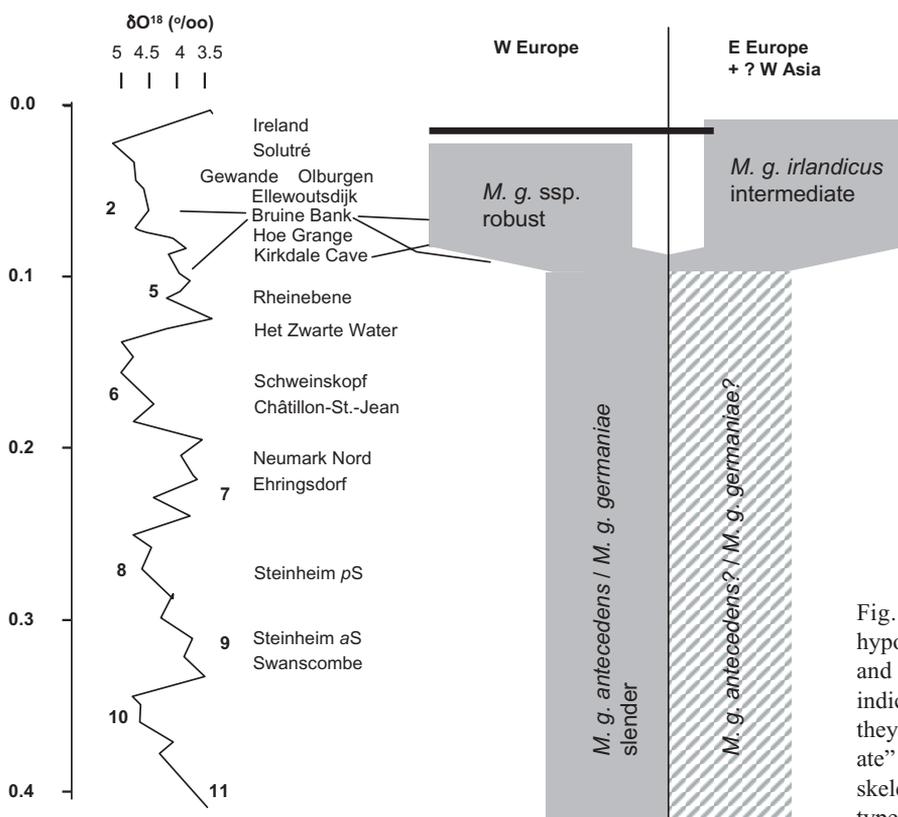


Fig. 10: Graphic representation of the hypothesis on *Megaloceros* biogeography and evolution. The available names are indicated, though this does not imply that they have priority. “Robust”, “intermediate” and “slender” refers to the post cranial skeleton and in particular to the morphotypes of metapodials discussed here.

me in any other way: G. BOSINSKI, E. CIOPPI, A. CURRANT, D. C. KALTHOFF, W. VON KOENIGSWALD, H. LUTZ, D. MANIA, H. MELLER, B. SÁNCHEZ CHILLÓN, J. DE VOS, R. VAN ZELST, R. ZIEGLER. The referees A. J. STUART and L. ABBAZZI and the editors R.-D. KAHLKE and P. MAZZA contributed with constructive criticism. I benefited from support by projects BOS2003-08938-C03-02 and CGL2004-04169/BTE and the “Unidades Asociadas” program of the CSIC.

## References

- AZANZA, B., & MORALES, J. (1989): Los artiodáctilos de Huélago, Huéscar-1 y Cúllar de Baza-1 (cuena de Guadix-Baza, Granada). — Trabajos sobre el Neogeno-Cuaternario, **11**: 289–315; Madrid.
- AZZAROLI, A. (1953): The deer of the Weybourn Crag and Forest Bed of Norfolk. — Bulletin of the British Museum of Natural History, Geology, **2** (1): 1–96; London.
- BERCKHEMER, F. (1941): Über die Riesenhirsche von Steinheim an der Murr. — Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **96**: 63–88; Stuttgart.
- BOSSCHA ERDBRINK, D. P. (1983): More fossil material of *Ovibos* from the Low Countries and the North Sea. — Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, **86** (1): 39–53; Amsterdam.
- BOSSCHA ERDBRINK, D. P. (1993a): From the bottom of the North Sea: acquisitions to three private collections. — Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, **96** (3): 253–270; Amsterdam.
- BOSSCHA ERDBRINK, D. P. (1993b): Sundry fossil bones of terrestrial mammals from the bottom of the North Sea. — Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, **96** (4): 427–448; Amsterdam.
- DE MULDER, E. F. J., GELUK, M. C., RITSEA, I. L., WESTERHOFF, W. E., & WONG, T. E. (2003): De ondergrond van Nederland. — 1–379; Groningen, Houten (Wolters-Noordhoff).
- DREES, M. (1986): Kritische kanttekeningen bij de naam “zwarte botten fauna”. — *Cranium*, **3** (2): 103–107; Utrecht.
- FRENTZEN, K., & SPEYER, C. (1928): Riesenhirsche aus dem Diluvium des Oberrheingebietes. — Mitteilungen der Badischen geologische Landesanstalt, **10** (1): 175–233; Freiburg i. Br.
- GUÉRIN, C. (1980): Les Rhinocéros (Mammalia, Perissodactyla) au Pléistocène Supérieur en Europe occidentale; comparaison avec les espèces actuelles. — Documents des Laboratoires de Géologie Lyon, **79** (1–3): 1–1185; Lyon.
- KAHLKE, H.-D. (1967): Die Cerviden-Reste aus den Kiesen von Süssenborn bei Weimar. — Paläontologische Abhandlungen, Abteilung A, **3** (3–4): 547–610; Berlin.
- KAHLKE, H.-D. (1968): Die Cerviden-Reste aus den Travertinen von Weimar-Ehringsdorf. — Paläontologische Abhandlungen, **23** (2): 201–249; Berlin.
- KAHLKE, H.-D. (1977): Die Cervidenreste aus den Travertinen von Taubach. — Quartärpaläontologie, **2**: 209–223; Berlin.
- KAHLKE, R.-D. (1999): The history of the origin, evolution and dispersal of the Late Pleistocene *Mammuthus* – *Coelodonta* faunal complex in Eurasia (large mammals). — 1–219; Rapid City, SD (FenskeCompanies).
- KERKHOFF, N., & MOL, D. (1991): Inventarisatie van Nederlandse vondsten van de muskussen, *Ovibos moschatus* (Zimmermann, 1780). — *Cranium*, **8** (2): 65–70; Utrecht.
- KOENIGSWALD, W. VON (1988): Paläoklimatische Aussage letztinterglazialer Säugetiere aus der nördlichen Oberrheinebene. — In: KOENIGSWALD, W. VON (Ed.): Zur Paläoklimatologie des letzten Interglazials im Nordteil der Oberrheinebene. — 205–314; Stuttgart, New York (Gustav Fischer Verlag).
- KOENIGSWALD, W. VON, & HEINRICH, W.-D. (1999): Mittelpleistozäne Säugetierfaunas aus Mitteleuropa – der Versuch einer biostratigraphischen Zuordnung. — *Kaupia*, **9**: 53–112; Darmstadt.
- KOLFSCHOTEN, T. VAN, & LABAN, C. (1995): Pleistocene terrestrial mammal faunas from the North Sea. — Mededelingen Rijks geologische Dienst, **52**: 135–151; Haarlem.
- KORTENBOUT VAN DER SLUIJS, G. (1957): Preliminary note on the first find of *Ovibos* in the Netherlands. — Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series B, **60** (2): 120–122; Amsterdam.
- KORTENBOUT VAN DER SLUIJS, G. (1985): Botten uit de Oosterschelde. — *Cranium*, **2** (1): 9–10; Utrecht.
- KUNST, C. E. (1937): Die Niederländische Pleistozänen Hirsche. — PhD thesis, University of Leiden: 1–126; Leiden.
- LISTER, A. M. (1994): The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). — Zoological Journal of the Linnean Society, **112**: 65–100; London.
- MADE, J. VAN DER (1989): The bovid *Pseudoeotragus seegrabensis* nov. gen. nov. sp. from the Aragonian (Miocene) of Seegraben near Leoben (Austria). — Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, serie B, **92** (3): 215–240; Amsterdam.
- MADE, J. VAN DER (1996): Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. — Contributions to Tertiary and Quaternary Geology, **33** (1–4): 3–254; Leiden.
- MADE, J. VAN DER (1999a): Ungulates from Atapuerca-TD6. — *Journal of Human Evolution*, **37** (3–4): 389–413; London.
- MADE, J. VAN DER (1999b): Artiodactyls del yacimiento mesopleistoceno de Galería (Sierra de Atapuerca). — In: CARBONELL, E., ROSAS, A., & DIEZ, C. (Eds.): Ocupaciones humanas y paleoecología del yacimiento de Galería. — 143–167; Valladolid (Junta de Castilla y León).
- MADE, J. VAN DER (2001): Les ongulés d’Atapuerca. Stratigraphie et biogéographie. — *L’Anthropologie*, **105** (1): 95–113; Paris.
- MADE, J. VAN DER (2004): *Megaloceros giganteus* from the Middle Pleistocene of Neumark Nord. — Veröffentlichungen des Landesamtes für Archäologie, **57**: 373–378; Halle.
- MADE, J. VAN DER (2005): La fauna del Pleistoceno europeo. — In: CARBONELL, E. (Ed.): Homínidos: las primeras ocupaciones de los continentes, Chapter 4 – Europa; Section 4.4. — 394–432; Barcelona (Editorial Ariel).
- PFEIFFER, T. (1999): Die Stellung von *Dama* (Cervidae, Mammalia) im System pleisometacarpaler Hirsche des Pleistozäns. Phylogenetische Rekonstruktion – Metrische Analyse. — *Courier Forschungsinstitut Senckenberg*, **211**: 1–218; Frankfurt.
- POHLIG, H. (1892): Monographie der *Elephas antiquus* Falc. führenden Travertine Thüringens, ihrer Fauna und Flora. II. Stück: Die Cerviden des thüringischen Diluvial-Travertines mit Beiträgen über andere diluviale und über recente Hirschformen. — *Palaeontographica*, **39**: 215–262; Stuttgart.
- REUMER, J. W. F., ROOK, L., VAN DER BORG, K., POST, K., MOL, D., & DE VOS, J. (2003): Late Pleistocene survival of the saber-toothed cat *Homotherium* in north western Europe. — *Journal of Vertebrate Paleontology*, **23** (1): 260–262; Northbrook.
- ROGER, O. (1887): Verzeichnis der bisher bekannten fossilen Säugetiere. — *Berichte des naturwissenschaftlichen Vereins Schwaben und Neuburg*, **29**: 1–162; Regensburg.
- STUART, A. J., KOSINTSEV, P. A., HIGHAM, T. F. G., & LISTER, A. M. (2004): Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. — *Nature*, **431**: 684–689; London.
- TURNER, E. (1990): Middle and Late Pleistocene Macrofaunas from the Neuwied Basin Region (Rhineland-Palatinate) of west Germany. — *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz*, **37**: 133–403; Mainz.
- TURNER, E. (1991): Pleistocene stratigraphy and vertebrate faunas from the Neuwied Basin region of Western Germany. — *Cranium*, **8** (1): 21–34; Utrecht.

Tab. 1: Measurements of the metacarpals of *Megaloceros giganteus* (in mm).

Locality	Collection	no.	DAPp	DTp	DAPpf	DTPf	DAPm	DTm	DTdist	III-DAP	III-DT	IV-DAP	IV-DT	L	L3	L4
Bruine Bank	Naturalis	133282	s	51.1	72.7	44.1	31.2	47.3	72.2	41.8	34.5	41.0	33.4	329.1	320.7	320.6
Bruine Bank	Naturalis	133402	s	43.9	64.6	39.9	27.4	42.3	67.3	39.5	31.9	39.7	31.0	307.6	299.0	298.0
Bruine Bank	Naturalis	138715	?	--	--	--	--	--	69.5	40.9	31.4	41.6	31.4	--	--	--
Bruine Bank	Naturalis	139583	s	43.9	≥63.3	--	31.2	41.5	62.9	>40.3	>27.9	>39.2	>27.8	334.7	325.2	325.9
Bruine Bank	Naturalis	147200	s	46.1	65.0	42.2	28.2	41.5	69.2	>37.7	>33.2	36.9	>31.1	289.2	282.4	280.3
Bruine Bank	Naturalis	152525	?	--	--	--	--	--	61.9	--	--	--	--	--	--	--
Bruine Bank	Naturalis	152646	s	--	--	--	31.6	--	75.1	45.1	35.2	44.1	34.0	--	--	--
Bruine Bank	Naturalis	153126	s	>45.5	≥67.1	≥40.4	28.9	46.1	≥67.8	>39.8	>31.9	>40.5	>30.3	302.1	292.6	293.2
Bruine Bank	Naturalis	153739	s	49.5	72.2	43.5	32.3	44.4	74.9	45.1	35.9	45.2	33.2	318.9	309.6	309.6
Bruine Bank	Naturalis	170032	s	42.2	62.8	39.4	29.7	38.5	68.4	40.9	32.9	40.8	31.1	308.5	299.9	299.5
Bruine Bank	Naturalis	172262	d	48.1	69.4	41.8	29.9	39.8	70.4	42.9	34.0	42.2	32.1	322.2	310.2	311.5
Bruine Bank	Naturalis	172286	d	50.0	68.1	~42.7	32.9	44.1	72.3	43.1	32.4	41.2	31.8	323.9	314.9	314.1
Bruine Bank	Naturalis	338449	s	42.7	61.1	38.0	29.2	37.5	64.8	40.3	32.2	38.9	29.5	316.9	307.0	306.4
Bruine Bank	Naturalis	338450	d	47.9	70.1	43.4	29.6	42.5	72.5	42.1	33.4	40.3	31.9	319.9	305.7	309.9
Bruine Bank	Naturalis	338453	d	44.5	65.0	42.4	29.7	42.3	69.9	41.9	33.4	41.8	31.2	313.6	302.2	303.8
Bruine Bank?	Naturalis	388149	s	≥43.7	62.9	≥41.1	29.2	41.3	68.4	>40.3	32.3	>44.1	30.3	333.7	325.3	324.9
Bruine Bank?	Naturalis	388150	s	47.7	65.9	42.1	30.8	46.2	72.2	42.4	34.9	40.9	32.7	320.9	311.5	309.8
Bruine Bank	Naturalis	388151	d	47.4	62.7	41.7	28.9	41.6	70.2	40.9	31.2	40.0	33.9	298.1	287.6	288.3
Bruine Bank	Naturalis	388964	d	50.9	76.2	--	30.9	48.7	77.8	44.0	35.1	43.6	34.9	311.3	303.4	304.5
Bruine Bank	Naturalis	400473	s	44.9	65.1	37.2	30.4	39.6	71.8	42.3	34.2	41.8	32.4	323.1	311.5	313.6
Bruine Bank	Naturalis	400474	s	44.9	69.2	40.8	32.6	39.3	≥73.6	41.7	34.5	--	--	324.2	315.6	--
Bruine Bank	Naturalis	400475	d	42.6	61.5	--	25.8	37.7	66.2	38.9	31.9	38.9	30.3	295.1	289.6	289.5
Bruine Bank	Naturalis	400476	d	46.9	66.5	39.9	29.7	41.4	68.9	43.2	33.2	42.4	31.9	306.6	296.1	296.4
Colijnsplaat	Naturalis	170048	?	--	--	--	~29.9	--	74.8	43.3	33.8	43.8	33.9	--	--	--
Ellewoudsdijk	Naturalis	79140	d	50.1	68.1	44.9	32.9	43.7	78.5	43.6	37.4	43.9	40.5	316.2	303.7	305.8
Ellewoudsdijk	Naturalis	19457	s	43.0	62.8	≥36.9	31.4	37.2	68.0	>39.7	33.1	>40.3	31.3	306.3	297.1	297.6
Rossum	Naturalis	138046	d	--	≥60.4	--	--	39.8	--	--	--	--	--	--	--	--
Olburgen	Naturalis	147375	s	44.8	63.5	40.8	27.9	38.2	67.2	40.3	32.4	40.4	30.4	316.7	306.7	307.1
Gewande	Naturalis	448990	s	50.9	70.8	43.5	31.9	42.7	76.9	45.0	36.5	44.9	35.9	322.7	309.8	312.6
Zwarte Water	Naturalis	118296	s	48.1	68.9	42.7	32.3	41.0	70.9	45.3	33.4	45.0	31.7	343.1	334.7	334.4
Zwarte Water	Naturalis	79265	d	--	--	--	26.9	--	66.7	44.0	32.3	42.7	30.1	347.1	>339.1	337.7
Rheinebene	NMM	PW1989/28	s	40.1	58.3	36.3	25.9	36.8	64.6	>39.2	29.8	≥39.2	30.5	342.8	331.9	353.6
Rheinebene	NMM	1957/357	s	43.5	63.8	41.0	28.5	39.7	65.1	40.9	30.0	40.1	30.2	337.4	328.8	330.5
Rheinebene	NMM	PW1989/27	s	≥38.1	59.2	≥32.4	27.9	38.7	≥60.0	>32.1	≥26.7	>34.0	≥26.3	311.8	305.5	304.0
Eich	NMM	1962/101	s	38.0	57.3	33.5	28.7	39.2	≥58.1	--	≥27.5	--	≥25.9	335.1	328.7	329.7
Eich-Büttel	NMM	1980/305	d	42.9	60.9	47.4	26.8	37.9	64.0	40.6	29.9	39.7	29.7	326.5	316.7	317.4
Gimbsheim	NMM	PW1997/707LS	d	43.8	61.2	39.3	30.2	35.7	~65.4	≥40.6	30.7	--	--	≥329.5	321.6	--
Eich	NMM	PW1988/404	d	41.1	60.8	36.3	25.5	38.9	63.9	39.6	30.3	38.9	27.7	321.9	313.9	314.5

Eich-Gimbsheim	NMM	PW1987/898	d	≥48.1	69.7	≥42.3	≥66.9	30.5	45.5	≥67.2		≥31.8	--	>28.3	338.3	329.3	331.5
Niestein/ Kornsand	NMM	1965/425	d	41.8	62.4	≥34.6	58.5	30.4	37.1	62.1	38.2	28.1	38.1	27.9	338.1	330.4	334.0
Eich	NMM	1963/55	d	41.8	68.6	39.1	59.1	27.3	39.5	65.8	37.8	30.5	37.9	30.3	322.0	314.2	314.0
Eich-Bürtel	NMM	1973/410	s	42.9	61.9	38.0	57.4	29.1	37.0	62.0	36.0	30.1	36.4	27.3	323.0	313.9	315.2
Eich-Minthe	NMM	E145	d	40.5	62.3	36.2	56.3	28.8	38.6	62.1	38.4	28.9	37.2	27.5	330.1	322.3	322.0
Rheinebene	NMM	B52	d	40.3	59.7	36.4	57.5	39.2	36.1	62.7	>37.8	28.6	37.6	28.4	326.9	319.2	320.3
Eich-Minthe	NMM	E142	d	>39.7	61.3	≥34.9	59.8	30.3	42.4	≥64.6	≥26.1	≥28.2	--	≥28.2	340.2	332.4	332.1
Rheinebene	NMM	B53	d	47.2	65.6	41.3	61.3	31.4	40.7	~72.8	41.8	33.9	--	--	325.9	316.6	--
Eich-Minthe?	NMM	E149(=?E139)	s	41.2	>56.7	≥34.6	--	25.1	37.7	62.1	37.8	29.0	38.4	28.9	312.7	305.6	304.1
Eich-Minthe	NMM	E143	d	43.3	63.4	38.2	58.9	27.9	38.7	64.6	41.2	29.8	40.1	29.2	331.8	319.9	322.2
Eich	NMM	PW1997/714LS	s	>42.7	65.0	≥39.9	62.1	34.1	45.6	>61	--	--	--	--	≥361.0	353.6	--
Gimbsh- Hubweise	NMM	PW1987/194	d	31.9	59.9	36.3	56.9	26.0	34.5	62.5	40.2	29.9	39.9	28.5	324.2	316.2	315.6
Eich-Gimbsheim	NMM	PW1987/896	s	38.3	58.1	33.6	56.4	28.1	37.6	59.9	--	≥26.7	--	≥26.3	321.8	313.6	314.4
Eich-Gimbsheim	NMM	PW1987/897	s	--	62.0	--	60.0	30.4	38.1	65.4	>39.0	31.9	>39.0	28.5	329.7	321.2	322.8
Eich-Minthe	NMM	1968/152	d	41.6	59.9	37.0	57.2	27.9	38.7	62.1	>36.8	29.1	>35.5	28.1	322.9	312.9	314.2
Eich-Minthe	NMM	1968/153	d	--	>54.1	--	>52.0	26.4	36.3	≥58.5	--	≥26.4	--	≥27.3	319.0	311.2	312.9

Plate 1

Metacarpals of *Megaloceros giganteus* from: 1) the Bruine Bank (40 miles west of IJmuiden; NNML 133282); 2) Gewande (NNML St 448990 = Gw106 = Gw 634); 3) Het Zwarte Water (NNML St 118296). Proximal (a), anterior (b), distal (c) and posterior (d) views.

