The giant deer *Megaloceros giganteus* is one of the most prominent species of the megafauna of the Pleistocene. It is particularly well known from Ireland, where during the 19th century many articulated skeletons were found in peat deposits. Hence the vernacular name »irish elk«.

*Megaloceros giganteus* is, as its name says, a giant deer and, along with the true elks, it is one of the largest deer known (Fig. 1). It reached a shoulder height of just over 2 metres. It was not as high as the living elk, but it was more stocky and it may have exceeded the maximum body weight of that species (about 500 kg). It was not only large, but also had very robust bones, in particular the metacarpals. However, not all »giant« deer were so large and some had sizes comparable to that of the red deer. Its most striking character are its large palmate antlers, which occasionally reached a span of over three and a half metres. It has even been suggested, that the large size of the antlers, which are lost and grow again each year, requiring an important amount of minerals, lead to the extinction of the species. However, it seems that the antlers have a normal proportion compared to body size. The palmate structure of the antler is also found in the fallow deer as well as several fossil species. However, also the brow tine (the first tine of the antler) is palmate, as is the case in the specimen from Neumark-Nord (Fig. 2). This is rarer, but occurs also in fossil deer, like *Megaloceros savini* and *Sinomegaceros*. Another characteristic is the pachyostosis in the mandibles; the deposition of extra layers of bone result in thickening of the mandible, which thus becomes more massive and more rounded. The function or reason of this is unknown, but it has been suggested that it has something to do with the storage of minerals for the growth of the large antlers.

**THE AFFINITIES OF MEGALOCEROS GIGANTEUS**

While many extinct Pleistocene species are known from fragmentary remains, numerous natural history museums have a mounted skeleton of the Irish elk on display. Nevertheless, its affinities are the subject of an ongoing debate. It is commonly believed to be related to other fossil deer, including other species of the same genus, such as *M. savini*, species included in a genus that some call *Megaceroides* and others *Praemegaceros*, and the genera *Sinomegaceros*, *Arvernoceros*, and *Orchonoceros*. Its palmated antlers suggested affinities to the living fallow deer (*Dama*), while other morphological features suggested affinities to the red deer (*Cervus elaphus*) (Lister 1994; Pfeiffer 1999). The phylogenetic relationships of living species of deer have been reliably reconstructed with the help of their DNA. The study of DNA of *Megaloceros giganteus* showed that it is related to the fallow deer (Lister et al. 2005).

Among the different kind of giant deer, some have brow tines that have a cylindrical section, like in most...
other deer. Or at least these are tines in the position of the brow tine, but they often had a little humb just above the burr. It seems that this is the remanant of a tine, which is present in geologically older samples. There is also a tendency in the geologically younger forms for this tine or humb to be totally absent, and even for the next tine to be absent. These are the deer which are often placed in *Megaceroides* or *Præmegaceros* and which lived in Europe and the Middle East between some 1.4 and 0.4 Ma ago, and which appeared about 0.15 Ma ago in the north of Africa (Part of the lineage is thus not represented in the fossil record). These deer had also robust metapodials.

The relationships of the giant deer with palmate browtines was recently studied by J. van der Made and H.-W. Tong (2008). *Sinomegaceros* of the east of Asia had also palmate browtines, but the palmation tends to be oriented vertically and in transverse direction. Though there are many similarities with *M. giganteus*, the east asian giant deer possibly goes back to *Arvernoceros* and thus has been separate branch for over three millions of years. The species most closely related to the Irish elk is *Megaloceros savini* of the early Middle Pleistocene of Europe, which is known from important localities like Süssenborn and Voigtstedt in Thüringen. It is a small »giant« deer, more or less the size of the red deer. It had a palmate brow tine, while the rest of the antler was not palmated, but branching. Unlike *M. giganteus*, but like *Sinomegaceros* it had metacarpals with a robusticity similar to those of the red deer. It acquired a series of masticatory adaptations (larger premolars smaller third molar, thicker molar enamel and a different articulation of the mandible with the skull), which suggest that it was on an evolutionary pathway divergent from that of *Megaloceros giganteus*. Though it was the most closely related species known, and lived in Europe till just before the appearance of *M. giganteus*, it was not the direct ancestor.

**THE ECOLOGY AND EXTINCTION OF MEGALOCEROS GIGANTEUS**

*Megaloceros giganteus* appeared in Europe some 400 ka ago by dispersal from some area in probably western Asia. Though its fossils are often found together with those of the mammoth and wooly rhinoceros, it does not seem to have been part of the typical glacial faunas of the so called mammoth steppe, which is an environment without present day analogue. Today there are vegetation belts that extend in east - west direction through northern Eurasia: the forests of the taiga, which are restricted to the south by aridity, give way to the steppe, and to the north by low light intensity, low temperatures and frozen soil in the winter, where they pass into the open landscapes of the tundra. During ice ages, temperatures drop and the tree line moves south,
till tundra and steppe fuse into one extensive environment, called the mammoth steppe (Guthrie 1990). This is believed to be an open environment, but with abundant vegetation, supporting a great biomass of mammoths, woolly rhinoceroses, musk oxen, reindeer, horses, saiga antelopes, etc. Many of these animals had a geographic distribution extending from the Atlantic coast of Europe to Alaska and even further into North America. *Megaloceros giganteus* did not form part of the typical glacial fauna, but it was not a typical "interglacial" species either and there is no fossil record of the southern parts of Spain, Italy and the Balkans. It lived in an area that extended from Spain till lake Baikal, while further to the east lived the giant deer *Sinomegaceros* (Kahlke 1994). *Megaloceros giganteus* seems to have preferred grass–shrub vegetation and open woodland with larch, spruce, pine and birch trees, but not the steppe–tundra with dwarf birches and willows (Stuart et al. 2004).

The Irish elk may have been a mixed feeder living in an open woodland or shrub environment. Although of moderate size, like other deer it has a preorbital fossa, which in the living species is known to contain a gland that is used to mark the territory. In the smaller Bovidae such glands have the same function, but larger species, which are not territorial but live in large mixed herds, lack these glands. In these bovid species, the females tend to have horns like the males. The closest analogue in cervids is the reindeer, which lives in herds and where females are antlered. Although *Megaloceros giganteus* is large, the males have preorbital fossas and the females lack antlers. It seems thus that, like most living species of deer it was territorial, at least during part of the year.

Like many other species of large mammals, the giant deer went extinct during the Late Pleistocene or Holocene. This extinction event is universally accepted, but its causes are much debated. Some believe that the spread of *Homo sapiens* caused the extinction through over hunting, fragmentation of the habitat, etc. Others believe that climatic and environmental change was the cause, or a combination of both. The extinction of the giant deer was studied in great detail by A.J. Stuart et al. (2004). It disappeared from western Europe during the last glacial maximum (about 20–12 ka), but survived in eastern Europe or western Asia and briefly reappeared in western Europe between 12.5 ka and some 10 ka. Its disappearance and reappearance seem to have been related to the presence of suitable environments with open woodland or shrub, while its final disappearance from Europe may have been related to the spread of *Homo sapiens*. In western Asia it survived till at least 7.7 ka. This chronological pattern could explain well a morphological pattern observed by A.M. Lister (1994). The early European *Megaloceros* had moderately robust limb bones, in particular the metapodials. It seems that in a short period during the early Late Pleistocene they became much more robust, while still later they were again a little more gracile. It seems that, while in western Europe *Megaloceros* became much more robust, in eastern Europe (or western Asia) it became only a little more robust, and that after the robust west European form became extinct 20 Ma ago, the relatively more slender forms from the east recolonized western Europe some 12.5 ka ago (Fig. 4; Van der Made 2006). No metacarpals are known from Neumark-Nord, but because of other characters (not discussed here), its giant deer was assigned to *Megaloceros giganteus antecedens*, the early subspecies with the least robust metacarpals (Van der Made 2003).

4 Model of the evolution of *Megaloceros giganteus* (after Van der Made 2006).

Literatur
Guthrie 1990

Kahlke 1994

Van der Made 2003

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Lister 1994

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