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What Does the Mass Accumulation of 100 Late Pleistocene Fallow Deer Skeletons (*Dama geiselana*) and Red Deer Skeletons (*Cervus elaphus*) from Neumark-Nord Reveal about the Cause of Death?

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Abstract

In the open-cast lignite mine of Neumark-Nord (Saxony-Anhalt, Germany, Eemian interglacial period) the richest fossil fallow deer material which has been found so far was collected. About 80 articulated skeletons and partial skeletons of *Dama geiselana* Pfeiffer, 1998 (Cervidae, Mammalia) and 20 partial skeletons of *Cervus elaphus* in perfect state of preservation were recovered, together with skeletons of *Elephas antiquus*, *Stephanorhinus kirchbergensis* and *hemitoechus*, *Bos primigenius*, and *Panthera leo spelea*. The extraordinary composition of the thanatocoenosis of the deer provided decisive information on the cause of death, which is presented here. The deer show the typical preservation of drowned carcasses; 75% of the deer skeletons belong to strong males, while juveniles and females are rare, and very old individuals are missing in the deer assemblage. Several disasters in different years have led to the mass occurrence of deer. The individual age determination of the juveniles, the stage of antler development, and the level of epiphyseal adhesion are explained here. They show that the majority most probably died in autumn. This information provided the crucial approach to investigate nitrifying toxic cyanobacterial blooms as a cause of death. The biochemical results obtained by absorption spectroscopy and RP-HPLC with UV-detection, published in 2002, showed that pigments, and probably toxins, characteristic of cyanobacteria are preserved in the sediment.

Keywords: Pleistocene, *Dama geiselana*, *Cervus elaphus*, Neumark-Nord, Eemian, skeletal morphology, mass death, individual age determination, toxic cyanobacterial bloom

1. Introduction

Brown coal mining during the years 1986–1996 in Neumark-Nord, situated at the northern periphery of the Geiseltal valley southwest of Halle (Saxony-Anhalt,

11°44'E, 51°21'N, **Figure 1**), exposed a Pleistocene lake basin yielding one of the most spectacular mass accumulations of fossil of large mammal skeletons that have ever been found. The dating of the locality was long disputed, formerly dated to an Intra Saalian interglacial period [1]; now dated to the Eemian [2–4].

Articulated skeletons and partial skeletons of 80 fossil fallow deer *Dama geiselana*, 20 red deer *Cervus elaphus*, 40 straight-tusked elephants *Elephas antiquus*, 8 aurochs *Bos primigenius*, 12 forest and steppe rhinos *Stephanorhinus kirchbergensis* and *hemitoechus*, and a cave lion *Panthera leo spelea* were recovered, indicating a warm to temperate climate. Under the direction of D. Mania, the “Working group Bilzingsleben” together with M. Thomae, the discoverer of the first large mammal skeletons, carried out the fieldwork of the site and the extensive evaluation of the results [1, 5–8].

The excavations had to be carried out parallel to the lignite mining work, often under time pressure in front of the approaching excavator. Numerous skeletons were cut by the excavator and could only be recovered incompletely. The brown coal mining company Braunsbedra employees are responsible for the recovery of many remains of skeletons, some of which were run over by the excavator. Often the excavator was stopped for the rescue of a skeleton. It is hard to estimate how many skeletons had been actually embedded in the sediments of the small lake of 300 by 500 m extension, before the lake was finally dredged in 1996. In addition, small mammals, birds, fishes, amphibians, reptiles, insects and other invertebrates, numerous plant megafossils, often with chlorophyll preservation, and abundant pollen occur in the finely laminated sediments.

In 2010, the Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt—Landesmuseum für Vorgeschichte Halle/Saale (LDA) dedicated a special exhibition named “Elefantenreich—eine Fossilwelt in Europa” (Elephant Kingdom—a fossil



Figure 1.
Neumark-Nord, site of a mass accumulation of large mammal skeletons, fallow deer were especially numerous.

world in Europe) to the extraordinary mass occurrence of straight-tusked elephants and the accompanied fauna and flora of Neumark-Nord, which was to be seen in several German cities in the following years. The accompanying volume to the exhibition summarizes the research results [9].

The morphology of the deer skeletons was studied intensively by Pfeiffer [10–12]. Ontogenetic stages, sexual dimorphism, and variation of bone and tooth features were examined. The variation range of the bone dimensions and proportions and the antler development in all ontogenetic stages could be determined. The fallow deer could be distinguished from the recent *Dama dama*, and was initially described as a fossil subspecies *Dama dama geiselana* Pfeiffer, 1998 [10], but upgraded later to species level *Dama geiselana* [13].

All fossil finds are housed in the LDA and recorded in the catalog. HK 87:300, 713–799, means, for example, that the skeleton was entered in the “Hallenser Katalog” (HK) in 1987 under numbers 300, 713–300, 799. The number of preserved skeletal elements can be seen that way.

2. The lake basin

The origin of the lake basin presumably was caused by depressions between coal ridges and probably was influenced by halotectonics [1, 5]. With the help of numerous vertical and three horizontal sections, Mania was able to reconstruct the three-dimensional structure of the deposits in the lake basin [8]: “The sedimentary sequence shows that the interglacial lake deposits could be dated to between the Groundmoraine of the Saale ice-age (Drenthestadum, Saalian I), and an older loess sequence (Saalian II, III). Over this lay a soil complex and the younger loess sequence (Weichselian) The analysis of the annual horizons of the organogenic sediments of the early and middle interglacial suggested a deposition process lasting 8.800 years.... There was then a middle interglacial lake phase (climatic optimum). This was interrupted by two regressions.... Each time however a small area of lake remained. The wide littoral zone, which was formed by the two major regressions, was the main finds horizon (**Figure 2**). The lake phases in the second half of the climatic optimum are marked by an intensive eutrophication and stronger salination of the lake.” All ecological zones from the littoral to the limnic profundal of the shallow lake are present. The high carbonate content of the warves (**Figure 3**) and the Neumark-Nord sediments in general afforded conditions for the preservation of calcareous invertebrate hardparts as well as phosphatic vertebrate bones and teeth.

Especially the fallow deer finds were concentrated in the coarse and fine detrital mud zone and algae mud zone of the site, which were deposited during the climate optimum of the interglacial period. Along with elephants, isolated red deer were also found in the deeper deposits of the first regression phase of the lake; red deer are also preserved in strata above the highly eutrophic strata indicating warm to moderate climate (**Figure 2**).

During deer’s lifetime, the landscape was open parkland, thermophilic trees such as the oak and hornbeam were abundant, and the shallow shoreline of the lake was characterized by reeds and a floating leaf belt. Special feature of the flora are proven halophytes indicating high salt concentrations [5, 14, 15]. Coal diapirism probably caused halotectonics in the lakeshore zone [1, 5]. Salt licks formed, which were extraordinarily attractive for large mammals. What was the doom in this pleasant landscape for so many deer? The skeletons themselves provided important clues.

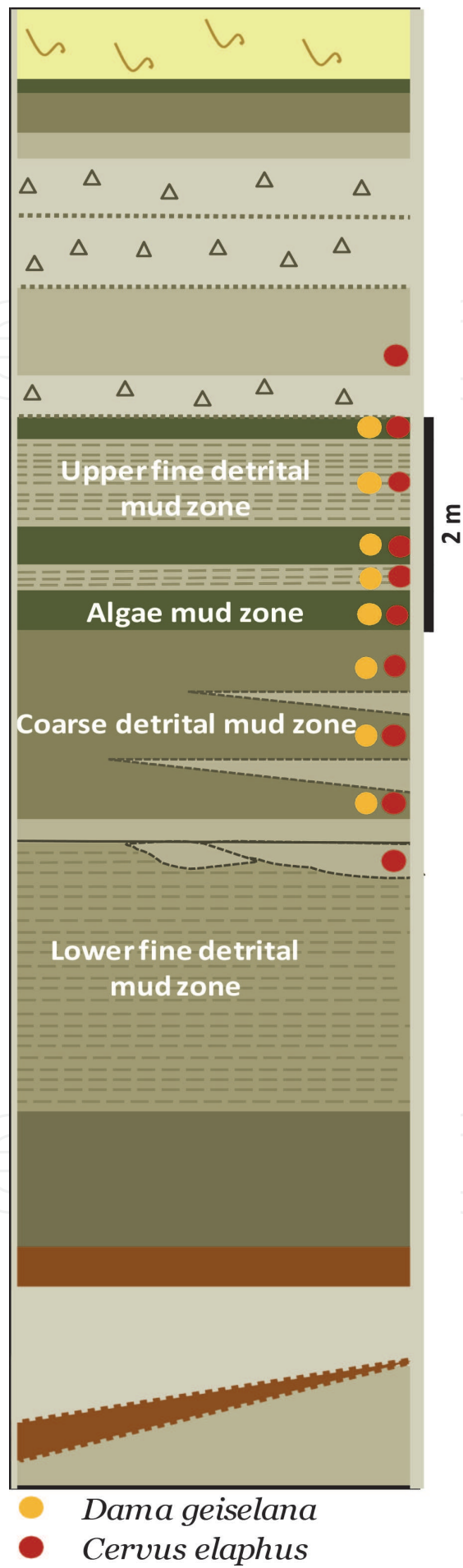


Figure 2.
Vertical sections of the interglacial lake sediments based on figures of Mania [5, 8]: fallow deer skeletons were especially numerous in the upper fine detrital mud zone and the algae mud zone.

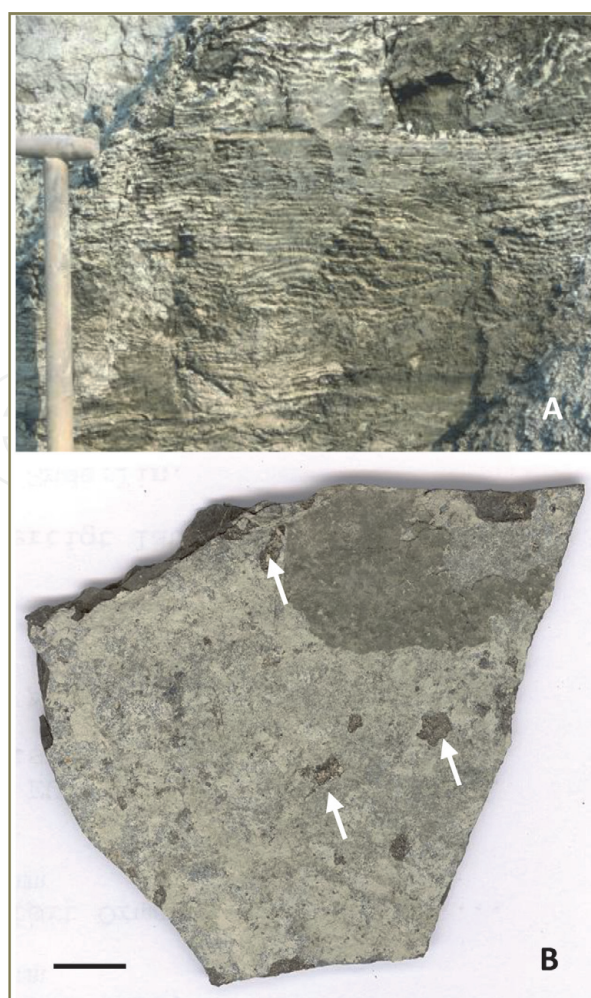


Figure 3.
A) Warves in the fine detrital mud zone. B) The carbonate portions of the warves appear to be cyanobacterial layers. The sediment is easily split at its boarder. The arrows mark leaf rests (scale bar 1 cm).

3. The find situation of the cervid skeletons

The 100 recovered deer were preserved as complete articulated skeletons or partial skeletons, many lying on the side with backwardly curved cervical spine and parallel leg position (**Figure 4**).

The skeletons were spread throughout the lake basin, few lay right on the shore (**Figure 5**). The actual number of embedded deer must have been much higher. On May 29, 1987, three skeletons, which were close to each other and were almost completely destroyed by the excavator, were detected by Mania in the coarse detrital mud zone. During an excavation with students, 17 cervids were found on May 22, 1989. The excavation work took place under unfavorable conditions in front of the approaching excavator. A month later, on June 21, 1989, Mania recorded 12 more fallow deer finds. All came from the fine detrital mud zone and showed the same state of preservation with two exceptions. The bones were very bright, slightly honey-yellow, and of firm consistency with a slightly glossy surface. On the other hand, skeletons of two subadult male deer with a brown surface must have come from another layer. There was no time to make sketches of the fallow deer skeletons in situ. The finds of these 2 days are marked with a box in **Figure 5**.

From 1994, finds of *Cervus elaphus* increase in frequency. The complete skeleton of a roughly 4-year-old red deer (HK 97: 14253) from March 13, 1995, which was discovered by members of the Paleontological Institute of the University of Bonn

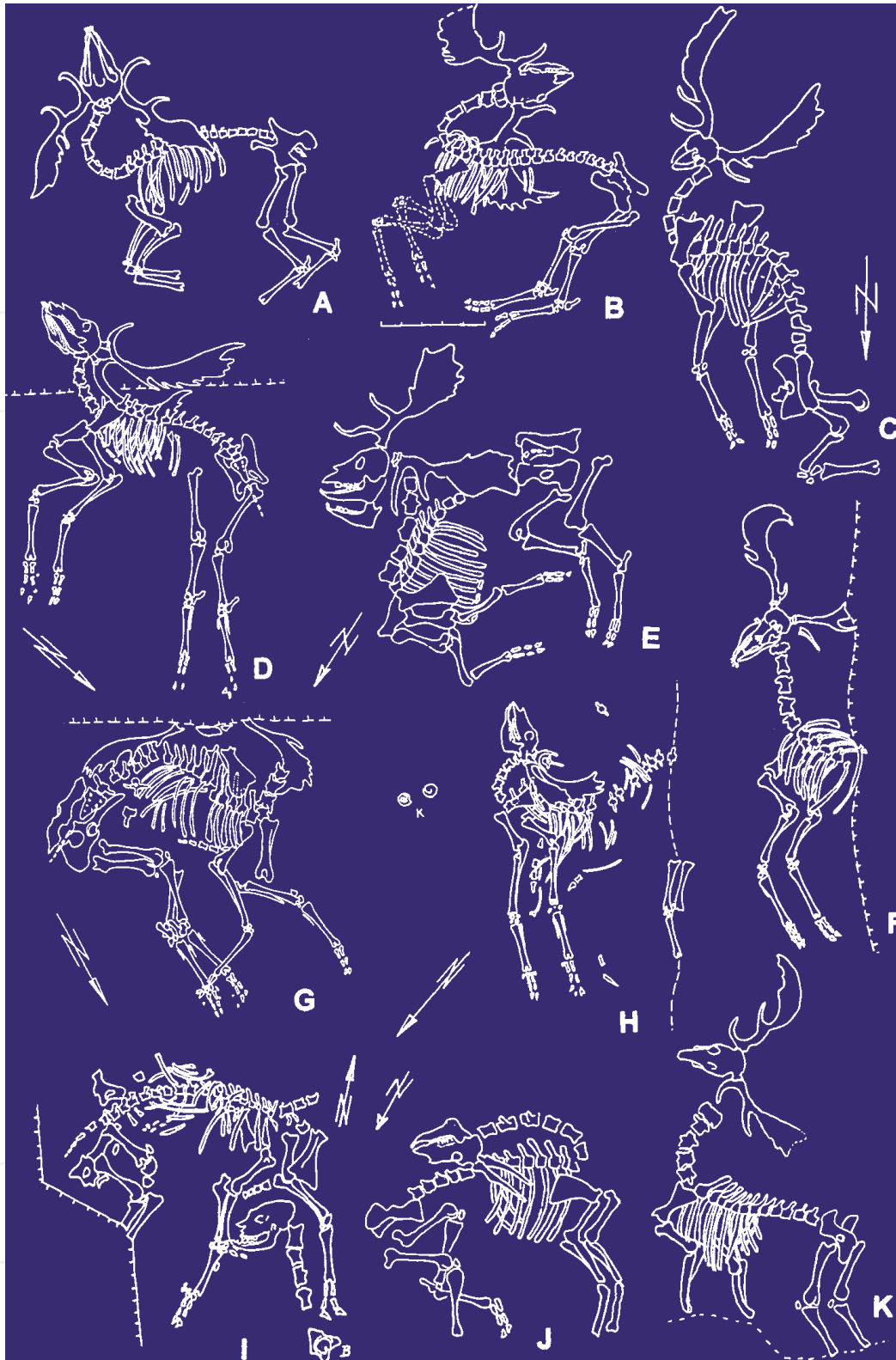


Figure 4.

*Fallow deer skeletons in embedding position based on sketches by Mania. The skeletons show the typical preservation of drowned carcasses. A–G) Skeletons of adult stags. C) Skeleton of the holotype of *Dama geiselana* HK97: 14165. F, K) Skeletons of subadult stags. H) Partial skeleton of a three year old stag with small antler blades. F, G, and H were cut by the excavator. I) Skeleton of a female with strong bite marks in the cervical spine (compare **Figure 8**). J) Skeleton of a juvenile stag with his first antlers (compare **Figure 12**).*

(including the author) during a visit to the site. It could be measured and photographed in situ (**Figure 6A**). The skeleton was articulated, with the rear body slumped deeper into the sediment; only the antlers and the skull were cut off from the excavator. This animal could be recovered intact. Another adult red deer (HK 97: 14254) was stuck about 3 m higher in the wall, already cut by the excavator, recovered as a partial skeleton on this day (**Figure 6B**).

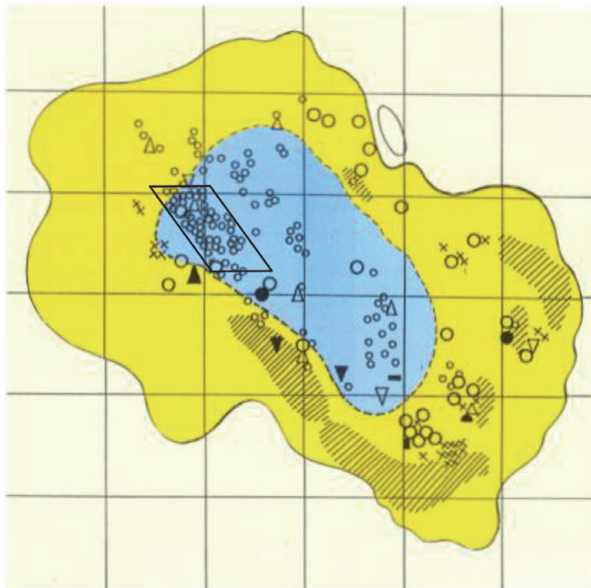


Figure 5.
Spread of the skeletons based on sketches from Mania. The box encloses the excavation area on May 22, 1989 and June 21, 1989; small empty dots mark deer skeletons.



Figure 6.
A) Red deer skeleton (HK 97: 14253) in situ, found on March 13, 1995. The skeleton was overrun by the excavator, skull and antlers cut off. B) Skeleton of an adult red deer (HK 97: 14254), sticking in the wall 3 m above the former skeleton and already cut by the excavator.

The majority of the skeletons were intact, without cut marks and further treatment by humans, but had numerous fresh fractures due to heavy sediment load or damage caused by the excavator. Human activities were mainly detected from



Figure 7.
Antler fragment of Dama geiselana with strong bite marks. The rest was accompanied with the female red deer skeleton HK: 97: 14147.

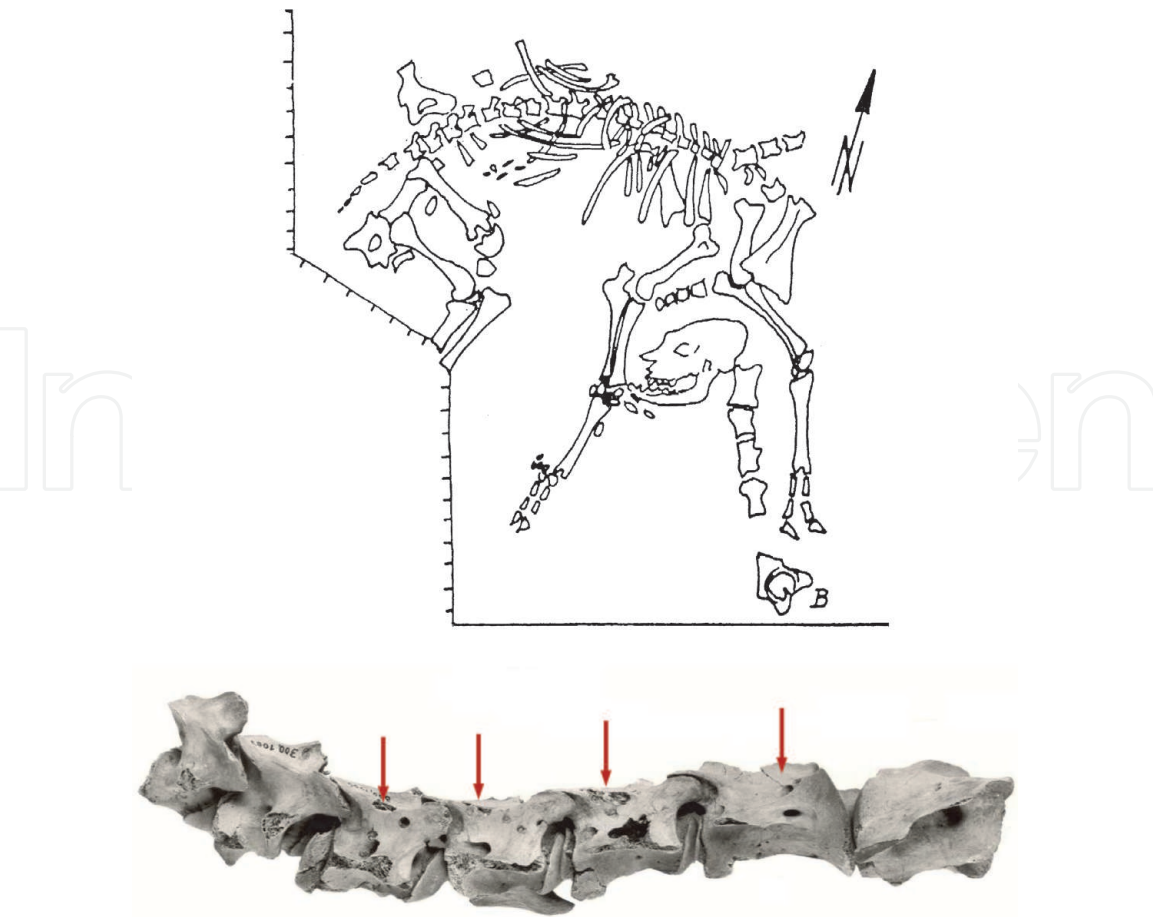


Figure 8.
The cervical spine of the juvenile female of Dama geiselana shows bite marks of a strong carnivore (arrows). The rest of the skeleton was articulated and undamaged, without gnawing marks.

the shore area of the lake's lower littoral zone, a zone from which many straight-tusked elephant skeletons originate. Mania was able to excavate clusters of silex artifacts in an area south and east of the lake. He documented a slaughter place with the skeletal remnants of an aurochs at the littoral edge of the lower littoral zone. The bones were often smashed, detached from the natural bone articulation, a completely different embedding situation than with the deer skeletons [16]. Gaudzinski-Windheuser [17] analyzed surface modifications on bones from complete cervid carcasses and attested the marginal exploitation of these resources by Neanderthals. She suggested an indication of scavenging by the Neanderthals on some individuals, coming from the lake shore area, though the carcasses showed no sign of disarticulation.

The hunting of deer can be assumed by some isolated battered and charred bones coming from the lake shore area. However, the vast majority of the articulated deer skeletons do not show any indication of human use.

The activity of predators could be proven in some cases. In 1991, the rear partial skeleton of a female deer *Cervus elaphus* (HK 97: 14147) was recovered, in the vicinity of which lay an antler remnant of a strong fallow deer. The burr shows gnawing marks of a strong carnivore, presumably a cave hyena or a cave lion (Figure 7).

The articulated skeleton of a juvenile female of *Dama geiselana* (HK 87: 300, 958-1046 and HK 87: 300, 1113-1114) has strong bite marks in the area of the cervical spine. The head and cervical vertebrae are detached from the body. However, the animal was not further disassembled and eaten by predators (Figure 8). There are no bite marks on the meat-carrying parts of the skeleton.

4. The composition of deer finds from Neumark-Nord

4.1 The composition of deer species

The recovered skeletons and partial skeletons of *Dama geiselana* represent 80 individuals, only 10 of which belong to females. Finds of single, isolated bones have been neglected. Mania was able to observe the destruction of four other skeletons during dredging. The isolated relics of *Dama geiselana* increase the minimum number of individuals by at least 10 and a maximum of 20.

Twenty individuals of *Cervus elaphus* could be clearly identified by complete skeletons, partial skeletons, and isolated rests, of which at least two, possibly three finds are partial skeletons of female animals. A very young animal is preserved only by a phalange (epiphyseal joint still visible) that cannot belong to any of the other older red deer. An antler rest of *Cervus elaphus* with characteristic terminal fork was not included in the minimum number of individuals [11]. Surprisingly, *Megaloceros giganteus* is represented only by an antler rest [18], *Capreolus* completely missing. The composition of the cervid finds from Neumark-Nord is shown in Figure 9A.

The find composition is extraordinary. The fossil fallow deer is a very rare element in the interglacial faunas of Central Europe, while the red deer is common in cold and warm stages [19, 20]. In Neumark-Nord, *Dama geiselana* represents 80% of distribution, only 20% are red deer.

4.2 The distribution between juveniles, females, and males

The distribution between the sexes is also unusual, 88% are males, only 12% are females. Even more unusual is the composition of the age structure of the deer (Figure 9B); 75% belong to robust males with well-developed antlers. About 25% of

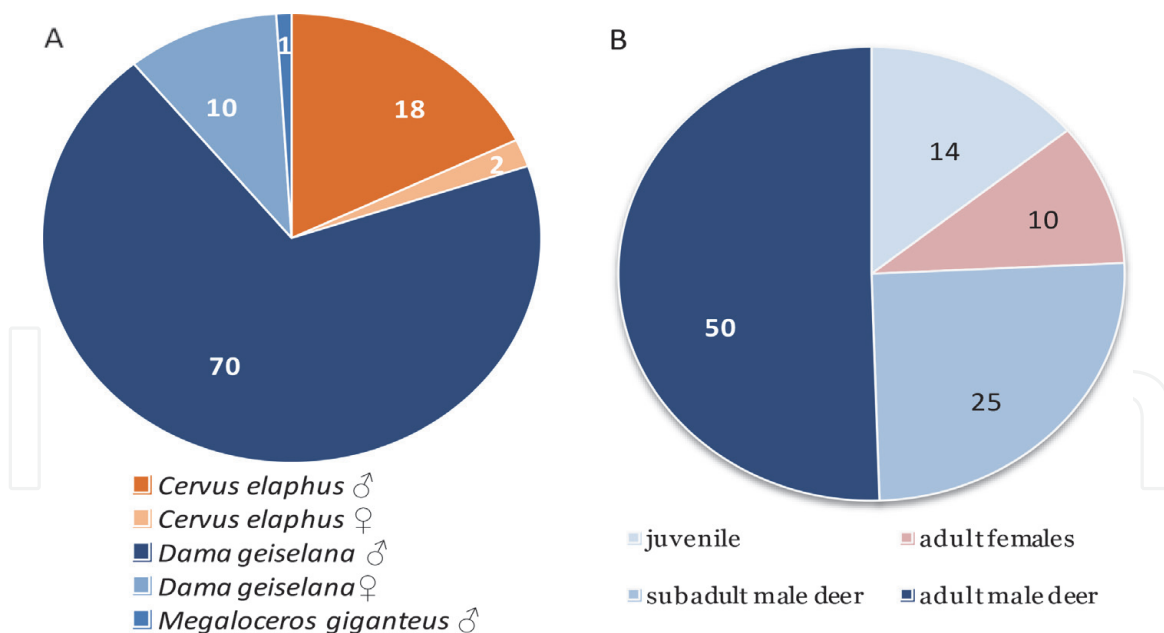


Figure 9.

A) Composition of the cervid finds. *Dama geiselana* is represented with 80 individuals, *Cervus elaphus* with 20. Females are underrepresented with only 12 individuals. From *Megaloceros giganteus*, only an antler fragment is preserved. B) The age structure shows that strong males (50) and subadult males, coming close to the adult stage (25), were especially frequent. Juveniles (14) and adult females (10) are clearly underrepresented.

the males were younger than 6 years at death (subadult), but they already had large antlers and came close to the adult stage. If no antlers are preserved, the subadult stage can be established on a series of non-fused epiphyses of the postcranial skeleton (see below). Only 9% of the skeletons belong to adult females, and only 14% belong to juvenile cervids including four juvenile females. The end of the juvenile stage is marked by the completed tooth change at the end of the second year of life. Very old individuals with worn teeth were totally lacking.

Assuming a natural mortality, the composition is most unlikely. Males and females should be evenly distributed. Inexperienced juveniles and very old animals should be frequent, and especially the young, strong stags should rarely be represented in the find material. The finding situation gives a clear indication that one or more catastrophic events led to the deer's death.

The question arises as to why the strong male animals are particularly affected. A crucial indication arose from the individual age determination of the deer, which allowed the death period to be limited for many skeletons to autumn, the rutting season of the deer.

5. Individual age determination

5.1 Individual age determination on teeth

Based on the knowledge that more than 90% of the fallow deer calves are born in the second half of June [21–23] the tooth status of the young animals can be used for the individual age determination (compare **Figure 10**). The method of tooth age determination in *Dama dama* is presented particularly well by Ueckermann and Hansen [23]. Illustrations used there are used here for the tooth age determination of fossil *Dama geiselana*. The permanent dentition is complete between the ages of 24 and 26 months, with the M_3 arising in the last 2 months of the second year of life. The deciduous premolars are changed this time.

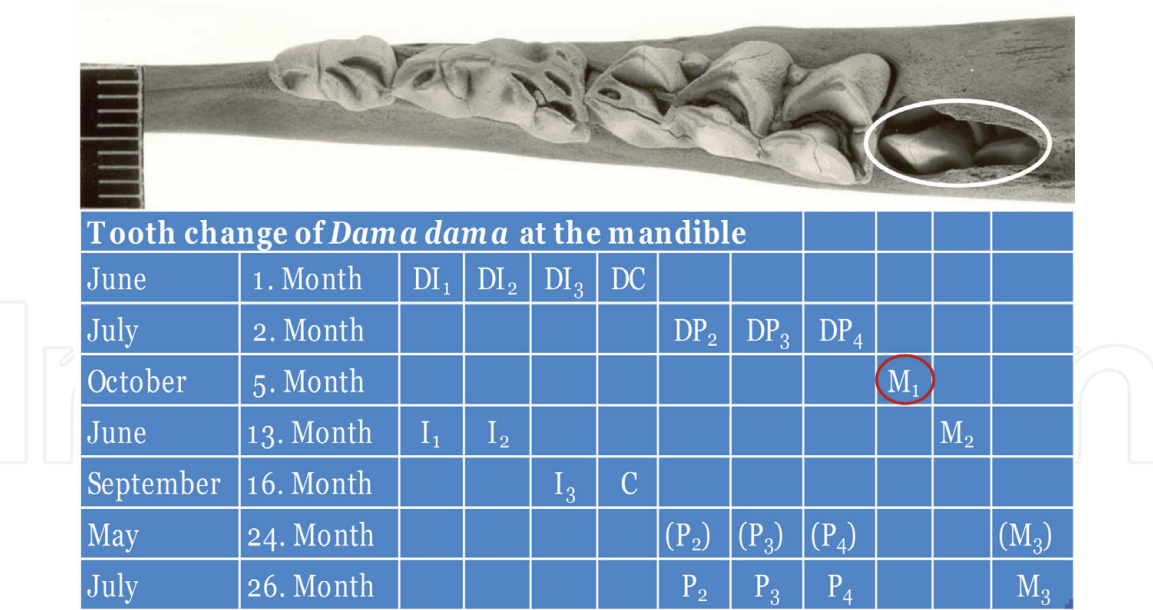


Figure 10.
Age determination based on the change of the teeth in *Dama dama*. An age of 4–5 months can be determined on this mandible of *Dama dama*. The M₁ was just breaking through.

After changing the teeth, an age assessment can be carried out on the degree of tooth wear. It is highly dependent on the amount of hard, silicate-rich plants in the food and becomes increasingly inaccurate after the age of 4. In the third year of life, the last lobe of M₃ is still completely covered by white enamel. With increasing age, the teeth are stressed during rumination, brown dentin emerges more and more. Enamel rings are formed, which can be used for age determination [24]. This method was additionally used.

In *Cervus elaphus*, the temporal sequence of the tooth change is different from that of *Dama dama* (**Figure 11**).

All deciduous teeth appear in the first months of life, the M₁ in the fourth month, usually in September. The first year of life ends with the appearance of the M₂. From the 14th to the 19th month, the incisors and the canine are successively changed. In the 21st month, the deciduous premolars are changed, the M₃ appears. In the 25th month, the permanent dentition is completely developed.

5.2 Individual age determination by the ossification of the epiphyses

On the basis of the level of epiphyseal adhesion, Pohlmeier [25] has established a calendar for the individual age determination of recent *Dama dama* (**Table 1**). Here, this calendar was applied to *Dama geiselana*.

There is a clear difference between the sexes. In the female skeletons all epiphyses are fused with 4 years except the thoracic vertebrae, the females are adult then. Observations on recent fallow deer have shown that females are successful with reproduction at the age of 3, in some cases they start at an age of 2 years [21, 23]. The males reach the optimum of physical development much later at the age of 11. They then have the heaviest and most impressive antlers. To adapt to the antler weight, the cervical vertebrae, the proximal humerus, radius, and ulna can grow significantly longer than in the females [11]. This allows determining the individual age also in male fallow deer skeletons whose skull is not preserved. Many epiphyses are joined in a chronological order in the second and third year of life. Therefore, for young fallow deer up to an age of 4, the time of death can be limited.

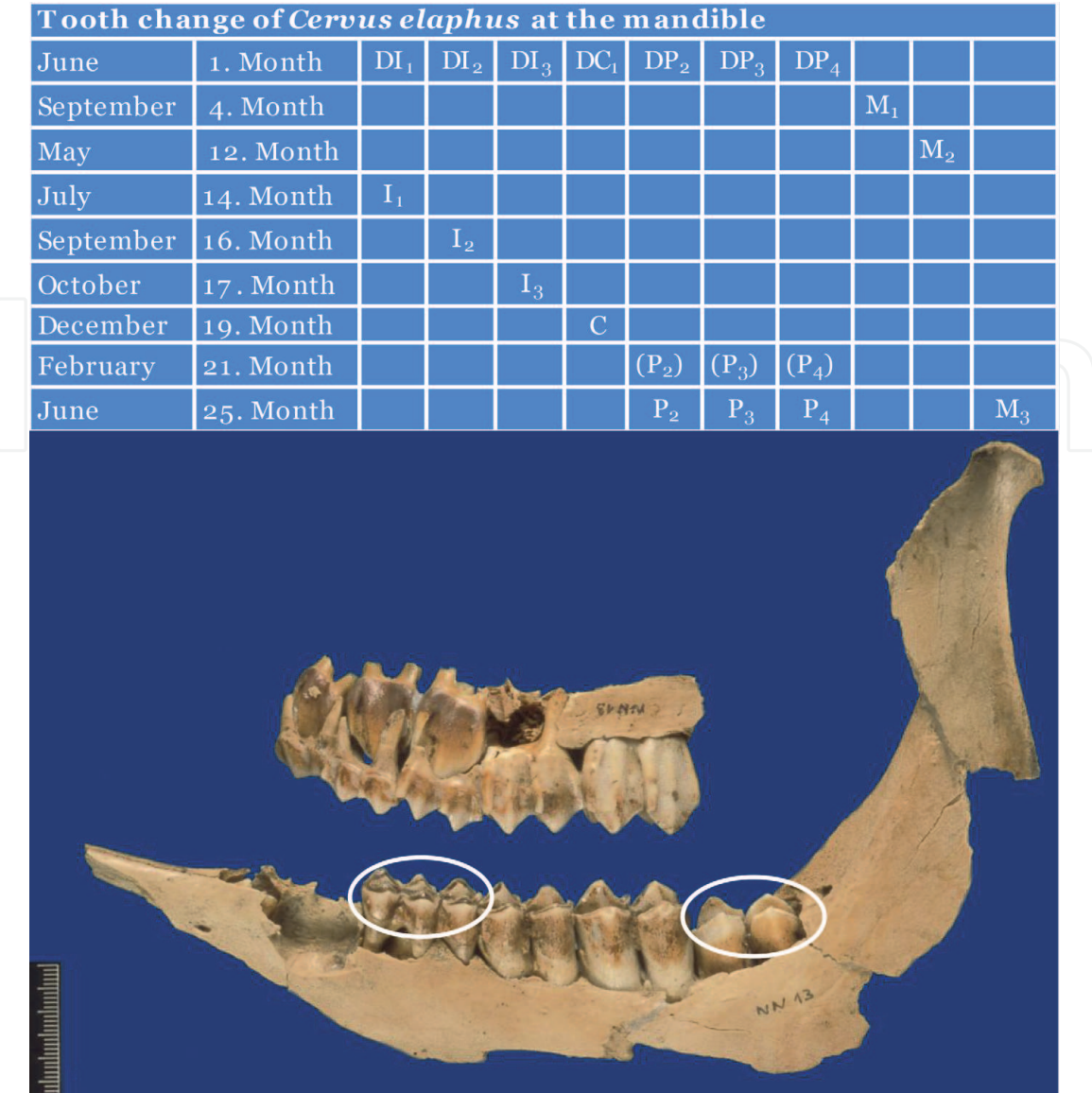


Figure 11. Tooth change of *Cervus elaphus*. In the juvenile female HK 97: 14161, the M₂ already shows slight wear (older than 12 months), the deciduous premolars have not yet changed (younger than 21 months), the M₃ just appears.

A 6-year-old stag can be well identified based on the ossified humerus epiphysis. From then on, the stags can be considered adult. The final shoulder height is reached, while the antlers increase in size and weight in the following years.

Fallow deer stags younger than 5 years can be identified by the lack of ossification at the epiphyses of the cervical vertebrae. They are classified as subadult. The ossification of the tuber coxae and the spina iliaca of the pelvis was completed at the age of 5, according to Pohlmeyer. In *Dama geiselana*, one significant difference was detected; the pelvic apophyses could be incompletely fused at the age of 8 years. This observation was also made in some recent fallow deer skeletons from Germany.

Fallow deer that are older than 9 years can be recognized by the complete ossification of thoracic vertebrae epiphyses and the pelvic symphysis.

There was no calendar of epiphyseal adhesion available for *Cervus elaphus*. Own observations on 23 recent skeletons with partly known individual age showed clear deviations from the fallow deer. The caput of MC III + IV and MT III + IV fuse at an age less than 2 years with the diaphysis, earlier than in *Dama*. The caput humeri

		Male ♂	Female ♀
Spinal column		data in month	
Atlas	disappearance of the joint cartilage in the median of the arcus dorsalis	22	22
Axis	caudal epiphysis	42 - 54	30 - 42
III-VII cervical vertebra	cranial and caudal epiphyses	42 - 54	30 - 42
Thoracal vertebrae	cranial and caudal epiphyses	84 - 108	84 - 108
Lumbar vertebrae	cranial and caudal epiphyses	12 - 36	12 - 36
Os sacrum	synostis vertebrarum sacrarum		
Vert. Sac. II, III and IV		6	6
Vert. Sac. I and II, III, IV		15 - 18	15 - 18
Thoracic bones			
Scapula	tuberculum supraglenoidale/ processus coracoideus	15	15
Humerus	caput humeri	72	36
	tuberculum majus	24	24
Radius	trochlea radii	24 - 28	24
Ulna	synostis ossium antebrachii	48	42
	tuber olecrani	22	22
	processus styloideus ulnae	24	24
MC III + IV	caput	24	24
Phalanx	proximal epiphysis	12 - 14	12 - 14
Pelvic bones			
Ilium	tuber coxae, spina iliaca dorsalis	60	38
Ischium	tuber ischiadicum	30	48
	adhesion of the symphysis pelvina	96	
	insertion of the os interischadicum into the symphysis	48	48
Femur	caput femoris, trochanter minor, distal epiphysis	22 - 24	22 - 24
Tibia	proximal epiphysis, tuberositas tibiae	27 - 28	27 - 28
Tarsal bones			
Calcaneus	tuber calcanei	23 - 24	23 - 24
MT III + IV	caput	22	22
Phalanx	proximal epiphysis	12 - 14	12 - 14

Table 1.
Age determination by the ossification of the epiphyses of *Dama dama* (data adopted from [25]).

fuses with the diaphysis about an age of 4 in males, much earlier than in fallow deer. The proximal and distal radius epiphyses fuse after completion of the fourth year of life in male red deer, much later than in *Dama*. At the same age, the tuber olecrani grows together with the ulna shaft. Also, the proximal tibia epiphysis and proximal and distal femur epiphyses do not fuse until 4 years of age. This level of development had reached the red deer skeleton HK 97: 14253, found on 1995, 13 March (**Figure 6A**).

As with *Dama*, the phalanges grow together at the beginning of the second year, cervical vertebrae in the fifth year of life, and thoracic vertebrae very late, from eighth year onward. These observations go well with the red deer from Neumark-Nord. However, the age assessment of the postcranial skeleton is not as well secured in the red deer as in *Dama*.

5.3 Age determination on antlers

The antler development in fallow and red deer is well studied [21–23]. The calves born in June develop the pedicle in the following February. On it grows a first antler without a burr, ending in a peak (**Figure 12**).



Figure 12.

Antler and atlas of a juvenile male of Dama geiselana (HK 97: 14154). The young stag had developed his first antler without a burr.

In April of the following year, the antlers are dropped off. Shortly thereafter begins the growth of a new, more complex antler. The second antler starts with a small burr, the diameter of which increases each year with the growth of a new antler. The pedicle is long and narrow in young individuals and gets shorter and wider each year with the increase in antler size. In *Dama* in the third year of life, a small antler blade evolves, which increases in size in the following years. The differences of the antler morphology between *Dama dama* and *Dama geiselana* are significant and discussed in detail by Pfeiffer [11, 13]. The optimum of antler development is reached in the eleventh to twelfth year of life. In the following years, the antlers of the very old deer are increasingly reduced to small peaks.

They can be clearly distinguished from juveniles by the strong burr. During growth, the antler bone is surrounded by a heavily perfumed skin. With completion



Figure 13.

Antler of an adult stag of *Dama geiselana* that was salvaged in fragmentary condition by employees of the coal mining company Braunsbedra in May 1995. The antlers show traces of rut fights. The first anterior tine looks polished; from the second anterior tine, the top is broken off, and the front edge of the antler blade shows numerous scratches (scale bar 10 cm).

of the antlers, the skin perishes and is stripped off. The antlers of robust males of *Cervus elaphus* were used in rutting fights in the period September to October and those of *Dama* in October. Traces of this can be seen in the anterior tines. They look polished, or have scores, or are broken off at the end. These conditions are typical of the antlers of strong stags in Neumark-Nord (**Figure 13**).

5.4 Age determination of the cervid skeletons of Neumark-Nord

5.4.1. Juveniles and subadult individuals of *Dama geiselana*

Only in three of the ten juvenile skeletons of *Dama geiselana*, the individual ages could be determined on the dentition.

- The juvenile female with the bite marks in the cervical vertebrae HK 87: 300,958-1056 already had a fully developed M₂, the DP₄ had not yet changed. That means, it was older than 13 months and younger than 24 months at death. With the only weakly fused epiphyses of the phalanges and the not-fused coracoid process of the scapula, the age could be further limited to 14–15 months; the time of death was in autumn.

- The young male of *Dama geiselana* HK 88: 2,1-72 died at the beginning of its third year of life. Its teeth show freshly raised premolars with M₃, still without wear. That indicates an age of minimum 26 months. The skeleton is very well preserved. The fully developed juvenile antlers confirm a death date in autumn.
- In the teeth of the juvenile male HK 97: 14151, the M₃ was just arising. This indicates an individual age of less than 2 years. The trochlea radii and the tuber olecrani were not fused, indicating an age of less than 22 months, a first antler was developed. This young fallow deer died in the spring.
- In a second juvenile female (HK 97: 14150), mainly the front limb was preserved. Teeth were not recovered, but the phalanges without any fusion of the epiphyses indicate an age of about 10 months. This young female died in spring. The skeleton was found together with the previous skeleton of the young male HK 97: 14151.
- HK 88: 4,1-59 is a juvenile male. No teeth are preserved. On the femur, an age younger than 22 months could be estimated, the phalange epiphyses were just growing together, the age was about 15 months. Time of death was in autumn.
- From HK 88: 17,7-14, only fragments are preserved of a juvenile male younger than 22 months, determined on the not-fused femur.
- The young male HK 97: 14194 was 15 month old, based on based on the not-fused tuber calcanei. Time of death was in autumn.

In the third year of life, the time of death can be limited by the fusion of the epiphyses of the proximal radius, the proximal tibia, and the lumbar vertebrae (compare **Table 1**).

With the proximal tibia, the time of death could be dated to the autumn in six young fallow deer (HK 88,2,1-72; HK 97: 14170; HK 97: 14174; HK 97: 14182; HK 97: 14183; HK 97: 14201).

HK 97: 14190; HK 97: 14197; and HK 97: 14158 are deer that died in the third year of life, but their skeletal elements are so incompletely preserved that one can only make the statement: little older than 2 years. They most probably died in autumn.

In the fourth year of life, the female fallow deer HK 97: 14164 died in autumn. This could be ascertained in the not-fused cervical vertebrae epiphyses (younger than 42 months) and the freshly fused caput humeri (older than 36 months). Also the female fallow deer HK 97: 14173 died in autumn at an age between 38 and 42 months, verified on the fused tuber coxae (38 months) and non-fused axis epiphysis (max. 42 months).

5.4.2. Adult males and females of *Dama geiselana* and *Cervus elaphus*

Although they are very complete, six female skeletons of *Dama geiselana* and one skeleton of a female of *Cervus elaphus* do not allow any statement about the period of death. All epiphyses are fused, the adult dentition is complete.

Stags of *Dama geiselana* with an individual age between 5 and 6 years can be well identified by the beginning fusion of the caput humeri, their antlers are already well developed. The time of death can be approximately determined by the development of the antlers. The same applies to fallow deer stags older than 6 years.

Their antlers were used in rutting fights as visible in signs of wear at the anterior antler tines and the front edge of the antler blades. The brow tine and the second anterior tine often look polished, or have scratches, or may be broken off at the end. In 20 fallow deer and 4 red deer, the antlers are preserved well enough to detect these traces (**Figure 13**). Therefore, the death period can be narrowed between October and February. In February, the antlers are dropped off.

5.4.3. Age determination in juveniles of *Cervus elaphus*

- In the juvenile female HK 97: 14161, the M₂ already shows slight wear (older than 12 months), the deciduous premolars have not yet changed (younger than 21 months), the M₃ is just breaking through (**Figure 11**). The time of death must have been between September and January in its second year of life. This age classification fits with the non-fused epiphyses of most long bones. MC III + IV and MT III + IV are fused distally, an indication that these epiphyses fuse earlier in *C. elaphus* than in *Dama*.
- In the skeleton of HK 97: 14161, coming from the lower fine detrital mud zone, the epiphyses of the long bones are not fused. Vertebrae of the sacrum are not completely ossified, confirming an age classification of 15–18 months. Period of death was in the autumn.
- The young male of *Cervus elaphus* HK 97: 14184 had just completed the change of teeth, the M₃ shows minimal wear. Its age is therefore at least 26–28 months, the time of death falls in the autumn. The age can be verified with the postcranial skeleton, most epiphyses of the long bones are not fused.
- The beginning of the fusion of the epiphysis of the caput femoris indicates a time of death in the beginning of the third year of life in the young stag HK 97: 14155.

6. Limitation of the death period

73 of the 100 deer skeletons from Neumark-Nord were included in the age determination. Isolated relics of dredged skeletons were neglected due to incompleteness.

In 13 young individuals of *Dama geiselana* and 4 juveniles of *Cervus elaphus*, the time of death could be determined quite precisely. Of these, 14 died definitely in autumn. Also 2 nearly adult females, and 2 juvenile males of *C. elaphus* definitely died in autumn (**Figure 14**). Two juvenile fallow deer died in the spring.

For most of the deer (44), the period of death was limited between September and January. Even with them, a death in autumn is probable. This group includes a juvenile red deer and three juvenile fallow deer, which most probably died in autumn. Twenty adult stags of *Dama geiselana* and four of *Cervus elaphus* have antlers with traces of rut fights. Out of 21 partial skeletons of adult male deer, only remnants of the antlers are preserved. They make it possible to limit the time of death between September and January.

Nine skeletons were complete enough to estimate the individual age in years, but they do not allow an indication of the death period. These include incomplete adult male skeletons without preserved antlers and the well preserved adult females.

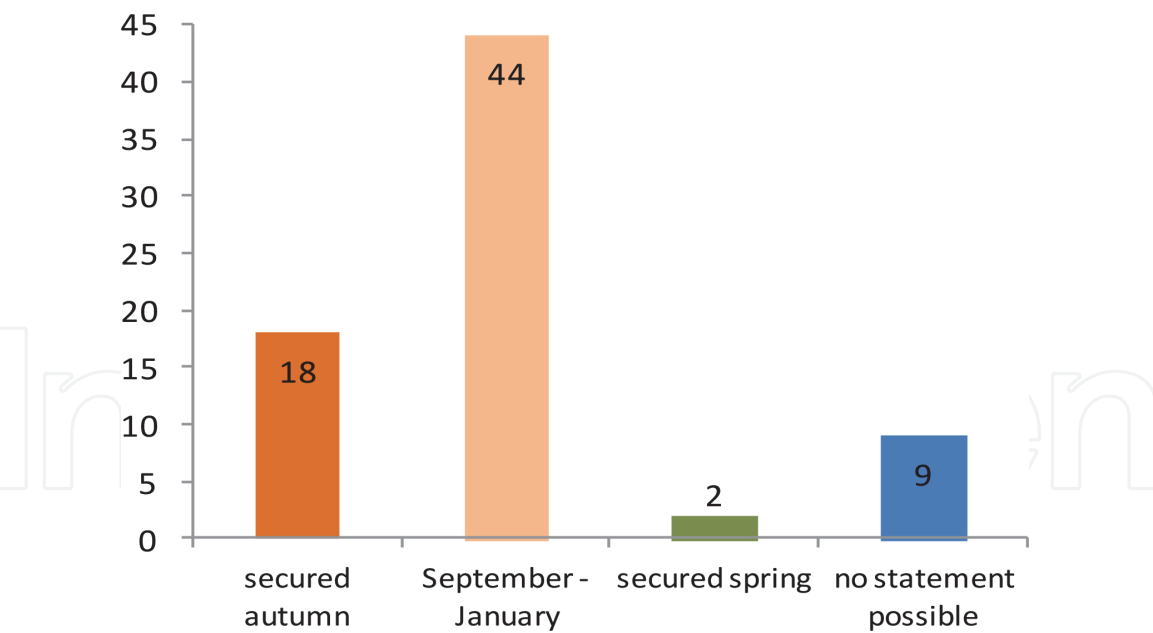


Figure 14. Limitation of the death period of 18, predominantly juvenile deer the time of death was in autumn, verified by the change of teeth and the degree of epiphyseal fusion. The second group (44) includes adult stags with antlers used in rut fights; they most probably died in the autumn. Two juveniles died in the spring. The last group includes the adult females. They also may have died in the autumn, but their skeletons do not allow any statement.

7. Discussion on the cause of death

The great frequency of complete or nearly complete skeletons repeatedly raised the question on the cause of death, and is discussed in the literature. Mania [5] as well as Bosinski [26] favored hunts of the deer of early humans before an analysis of the deer skeletons was made. The observation that most cervids died in the rut fighting season contradicts the hunting hypothesis; in autumn, male deer do not live together in herds. Humans would have dissected and eaten the hunted prey. But most skeletons are intact, without traces of cut marks or further treatment by humans.

Could the animals have broken into thin ice during the winter? This hypothesis cannot be completely excluded for the adult deer whose death period is determined only by the fully developed antlers. Deer with large antlers could get out of this situation worse than females without antlers. However, the occurrence of heat-loving plants speaks against the occurrence of hard frosts during the climatic optimum of the interglacial period of Neumark-Nord.

Also predators are not the cause of the deer mass accumulation. Only few skeletal elements show bite marks (see above). Even the juvenile female HK 87: 300, 958-1046 (**Figure 8**) with strong bite marks in the cervical spine was not eaten up either.

Poisoning by a gas cloud or gas eruption can be excluded. The lake was shallow, not more than 5–15 m deep, the pressure of the water column was not high enough to make a gas eruption likely [11].

The composition of the taphocoenosis speaks for several disasters in autumn in different years with varying intensity over a period of possibly more than 300 years during the climatic optimum of the interglacial period. Mania [1] estimated this time span on the basis of warve counts.

Pfeiffer suggested that toxic cyanobacterial blooms in the water poisoned the deer [11, 15, 17, 27, 28], the main arguments are repeated here.

Cyanobacteria of the genera *Anabaena*, *Microcystis*, *Nodularia*, *Nostoc*, and *Oscillatoria* produce hepatotoxic microcystins and neurotoxic anatoxins that can kill large mammals within a few hours [29, 30]. Microcystins have been responsible worldwide for repeated cases of thickness and death in pets and wildlife after ingestion of water containing toxic cyanobacteria [31–35]. From Germany, several cases have been described in recent years under comparable climatic conditions as in Neumark-Nord [36–39].

The poisonous effect of a cyanobacterial bloom was first described by Francis in 1878 in *Nature* [40]: “Being very light, it floats on the water except during breezes, when it becomes diffused. Thus floating, it is wafted to the lee shores, ... it is swallowed by cattle when drinking, especially such as suck their drink at the surface like horses. This acts poisonously, and rapidly causes death.” Hennig and Kohl [39] showed that the highest toxicity is reached when the cyanobacteria cells die, degenerate, and set the included poison free.

Park et al. [32] showed seasonal variations of *Microcystis* ssp. in Lake Suwa and found a second blooming period in October after the first bloom in spring. After the death of a summer algal bloom, much nitrogen is removed from the water. In spring, the selective advantage of cyanobacteria is achieved by the inhibition of eukaryotic algae, in autumn by nitrification (**Figure 15A**). Therefore, the two juvenile fallow deer who died in the spring may also have been victims of cyanobacteria toxins.

The sinking bloom of eukaryotic algae together with the generally high organic content of the water caused poor light penetration in the lake and favored nitrogen-fixing cyanobacteria drifting near the surface with the aid of gas vacuoles. During some sunny days in autumn, they can multiply explosively (**Figure 15B, C**) [29–32].

That cyanobacteria could be responsible for the mass accumulation of the deer was confirmed by investigations of the sediment [27].

The carbonate portions of the warves (**Figure 3C**) appear to be cyanobacterial layers that have been decomposed and deposited above a layer of chrysophycean cysts, which belong to the summer algal bloom. The distinct separation of the chrysophycean cyst layers from the overlying microbial carbonate layers indicates that the bloom of chrysophyceans was separated in time from that of the cyanobacteria and their subsequent calcification. The sediment is easily split between the two layers.

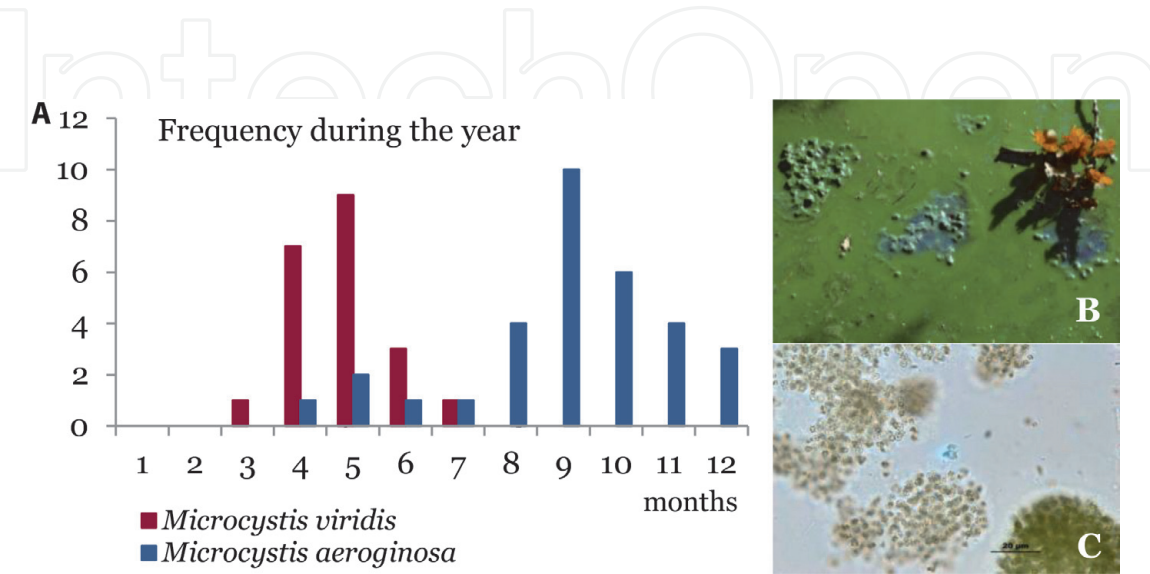


Figure 15.
A) Seasonal variation in *Microcystis* spp. (graph based on data from Park et al. [32]). *M. viridis* is dominant in spring, *M. aeruginosa* in the autumn. B and C: Bloom of *Microcystis* sp. in a small shallow lake in Riddagshauen (Germany, Lower-Saxony) on October 6, 2012.

The biochemical results obtained by absorption spectroscopy and RP-HPLC with UV-detection showed that photosynthetic pigments, and probably toxins, characteristic of cyanobacteria were preserved in the sediment [11, 27]. The results of the study of Braun and Pfeiffer [27] indicated the presence in the lake of large amounts of toxic cyanobacteria that most probably occurred in seasonal blooms.

In autumn, the following scenario may have occurred repeatedly in different years at the Pleistocene lake of Neumark-Nord.

Salt licks in the lakeshore region had made the area extremely interesting for large herbivores. A stag that has occupied such an area will be extremely attractive to an incoming female herd. The possible reproductive success causes the stags to embittered rut fights. Considering that only about 10% of the stags are involved in reproduction in their lifetime [21, 23], it takes a tremendous amount of effort to occupy the area. If they succeed, they will be the father of the entire subsequent generation of calves of the female herd.

Stags, being especially thirsty after their rut fights, would have been tempted to drink profusely from the lake. They do not dunk their nose while drinking to be able to smell predators. The toxic bloom is odorless [30], so they do not smell the danger. Thus, while drinking, the stags may easily have taken up a lethal dose of the cyanobacteria drifting near the water surface.

Females pay little attention to the rut fights. They were not forced to increase their water intake. They get the most liquid from juicy plant food [21, 22]. This explains why they are so rarely found among the victims.

Anatoxins and microcystins cause a rapid immobilization [31, 32, 41]. Before they died, the deer could not get far from the shore.

Most of the deer skeletons display the preservation typical of water carcasses, with parallel leg position and recurved neck, as evidenced, for example, from the Eocene site of Messel [42]. This could have happened as follows:

Higher rainfall in the late autumn will have led to an increase in the lake's water level. After death in the lake shore area many carcasses, inflated by digester gases, will be washed into the lake and distributed over the whole lake. With increasing decay the abdominal cavity broke open, the digester gases escaped, and the carcasses sank to the bottom of the lake. Then, the antlers acted as anchors, which got caught in the bottom sediment. The slack body came to rest beneath the head in side position. The cervical spine, twisted in many skeletons, can be explained in this way. In addition, the tensile force of the ligamentum nuchae caused a recurved neck, as it remained intact longer during decay than the antagonistic muscles.

Embedding in the sediment took place at a time when the skeletons were still clearly surrounded by soft tissues, because the bones are preserved in articulation.

Carcasses poisoned by cyanobacteria are spurned by predators. Should a scavenger tackle a poisoned animal, he quickly abandons it [30]. In Neumark-Nord, this was observed in the juvenile female HK 87: 300, 958-1046 (**Figure 8**). Although the animal has strong bite marks in the cervical spine, it was not eaten up, as the undamaged meat-bearing bones show.

Even the few skeletons from the lakeshore that have cut marks of stone tools [17] were not completely disassembled by the Neanderthals; may be the danger was recognized.

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Conflict of interest


The author declares no conflict of interests.

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