During the Pleistocene, there were three main groups of rhinoceroses, each of them in a different part of the Old World: the African lineage leads to the modern square-lipped rhinoceros and black rhinoceros, the Asian group includes the great one-horned rhinoceros, the Sumatra rhinoceros and the Java rhinoceros as well as their ancestors. The third group, which became extinct in the Late Pleistocene, includes *Coelodonta* and *Stephanorhinus.* The woolly rhinoceros (*Coelodonta antiquitatis*) appeared in Europe for the first time during the Elsterian cold period. *Stephanorhinus kirchbergensis*, the forest rhinoceros, is limited to the interglacial periods and probably dispersed again and again after each cold period from Asia into Europe. The steppe rhinoceros (*Stephanorhinus hemitoechus*) again has been present in Europe for 450,000 years. All three types of rhinoceros together could be documented in Neumark-Nord, which is even more astonishing, as the woolly rhinoceros generally is considered to belong to the glacial fauna. Remarkably, from the molars of the rhinoceros from Neumark-Nord plant remains were recovered. It could be proven that the food of the forest rhinoceros included Betulaceae, Rosaceae and grasses and, in particular, from poplars, oaks, hawthorns, pyracanthas, stinging nettles and water lilies. Unfortunately, no food remains could be identified from the steppe rhinoceros and the woolly rhinoceros.

Im Pleistozän traten drei Hauptgruppen von Nashörnern auf, jede in einem anderen Teil der Alten Welt: die afrikanische Linie führt zu den heutigen Breitmaul- und Spitzmaulnashörnern, die asiatische Gruppe umfasst das Panzer-, das Sumatra- und das Javanashorn sowie ihre Vorfahren. Zur dritten Gruppe, die im späten Pleistozän ausstarb, gehören *Coelodonta* und *Stephanorhinus*. Das Wollhaarnashorn (*Coelodonta antiquitatis*) trat in Europa zum ersten Mal während der Elsterkaltzeit auf. *Stephanorhinus kirchbergensis*, das Waldnashorn, ist auf die Interglaziale beschränkt und wanderte wahrscheinlich nach jeder Kaltzeit erneut von Asien aus ein. Das Steppennashorn (*Stephanorhinus hemitoechus*) ist wiederum in Europa seit 450 000 Jahren heimisch. In Neumark-Nord konnten diese drei Nashörner zusammen nachgewiesen werden, was umso bemerkenswerter ist, weil das Wollhaarnashorn im Allgemeinen als Vertreter der Glazialfaunen gilt. Als Besonderheit wurden aus den Backenzähnen der Nashörner von Neumark-Nord noch pflanzliche Nahrungsreste geborgen. Als Nahrung der Waldnashörner konnten Reste von Birkengewächsen, Rosengewächsen und Gräsern sowie insbesondere von Pappeln, Eichen, Weißdornen, Feuerdornen, Brennnesseln und Seerosen festgestellt werden. Bedauerlicherweise war es nicht möglich, vom Steppennashorn und vom Wollhaarnashorn Nahrungsreste zu identifizieren.

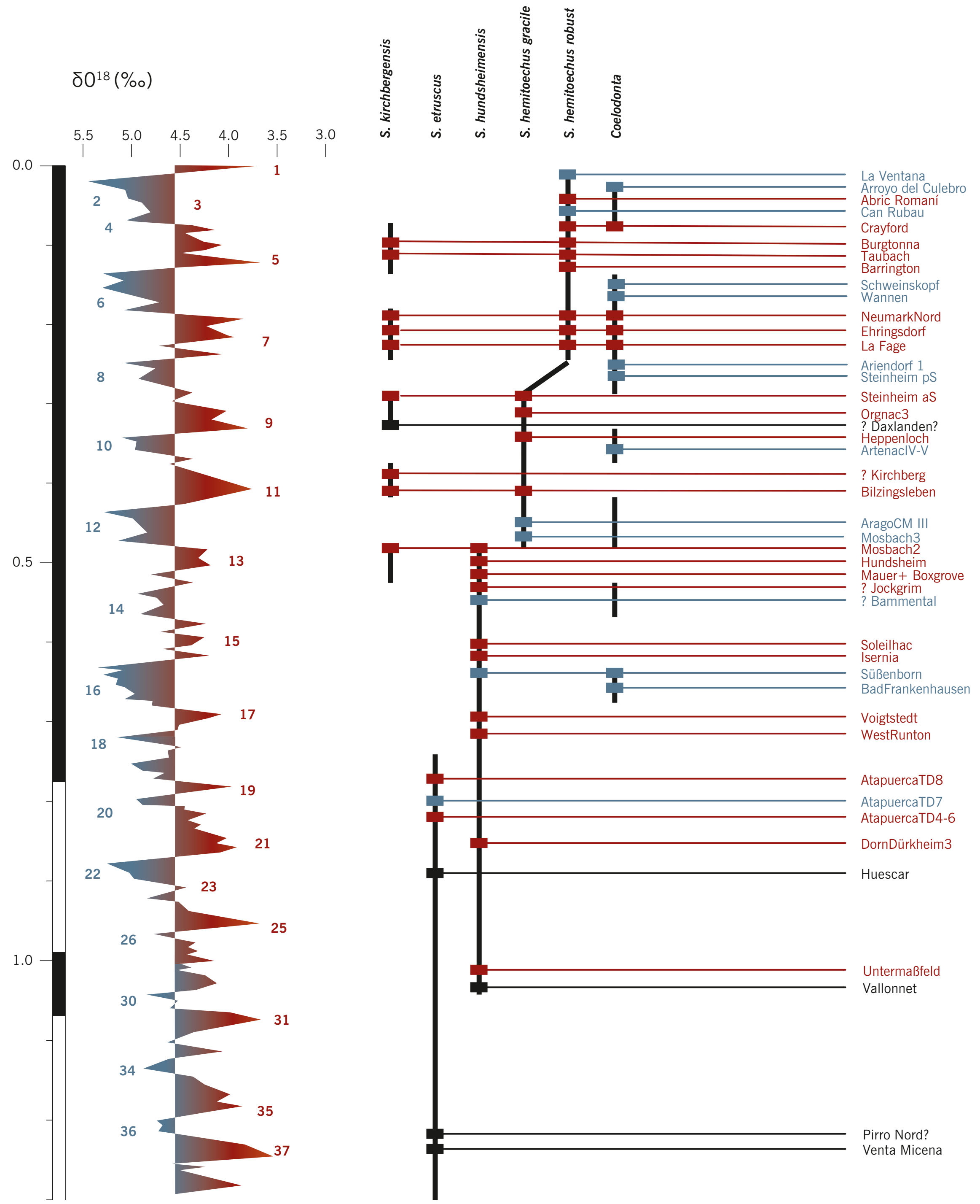
THE RHINOCEROSES FROM NEUMARK-NORD AND THEIR NUTRITION

DIE NASHÖRNER VON NEUMARK-NORD UND IHRE ERNÄHRUNG

Jan van der Made and René Grube

Rhinoceroses are mammals that share a number of characters, such as hoofs, and have an odd number of them per hand or foot, as well as cheek teeth with a typical pattern of crests. Contrary to what one might expect, horns were not present in many species of rhinoceroses.

The family Rhinocerotidae originated in the Middle Eocene of North America and spread by the Late Eocene to Asia (Cerdeño 1998). At that time Europe was isolated from Asia by a sea way. When, at the beginning of the Oligocene, some 33 million years ago, tectonics and sea level fluctuations caused the establishment of a land connection, many kinds of mammals dispersed from Asia into Europe, including the rhinoceroses. This is an important event, called the Grande Coupure. In a similar way, the Middle East started to become land, intermittently connecting Africa and Eurasia, allowing during the Early Miocene, around 20 Ma ago, the rhinoceroses to reach Africa and little later proboscideans to reach Europe. Rhinoceroses never reached South America, or Australia. Rhinoceros diversity reached a peak during the Miocene. The family went extinct in North America at the beginning of the Pliocene, about 5 million years ago. In Europe diversity started



1

The stratigraphic distribution of the European Pleistocene rhinoceroses.
Age in millions of years, palaeomagentism and Oxygen Isotope Stages on the left; temporal distribution of the rhinos indicated with black lines in the central part of the figure; localities on the right. Horizontal bars indicate presence of a species in a locality. Blue indicates presumably glacial and red interglacial localities. Question marks in front of a locality name indicate uncertainty about the stratigraphic position and a question mark behind a name indicates uncertainty about the taxonomic identification. The figure differs from earlier versions in that Mosbach 2 is placed one climatic cycle higher, because of doubts on the differences between deer from Mauer and Mosbach 2 and because of the recognition of assemblages with *Equus suessenbornensis* and *Arvicola*, which should be older than Mosbach and younger than Süßenborn.

Die stratigraphische Verteilung der Europäischen Nashörner aus dem Pleistozän.
Jahresangaben in Millionen Jahren, Paläomagnetismus und Sauerstoffisotopenstufen links, die zeitliche Verteilung der Nashörner ist mit schwarzen Linien in der Mitte der Darstellung angezeigt, Fundorte auf der rechten Seite. Horizontale Linien geben das Vorkommen einer Spezies an einem Ort an. Blau markierte Fundorte sind vermutlich glazialen, rot markierte interglazialen Charakters. Fragezeichen vor einem Ortsnamen bedeuten Unsicherheit in der stratigraphischen Lage und ein Fragezeichen hinter einem Namen bedeutet Unsicherheit in der taxonomischen Identifikation. Die Darstellung unterscheidet sich von früheren Versionen dadurch, dass Mosbach 2 aufgrund von Zweifeln an den Unterschieden zwischen den Rehen von Mauer und Mosbach 2 sowie bekannt gewordener Vergesellschaftungen mit *Equus suessenbornensis* und *Arvicola*, die älter als Mosbach und jünger als Süßenborn sein dürften, einen klimatischen Zyklus höher platziert ist.

to decline after the early Late Miocene (Heissig 1999) and they went extinct around the Pleisto-Holocene transition.

Rhinoceroses tend to be large and some species are among the largest land mammals that existed, with maximum body weights of up to 15–20 tonnes (Fortelius/Kappelman 1993).

Three major groups of rhinos occurred in the Pleistocene, each one in a different part of the Old World: Africa, southern Asia, and northern Eurasia. The African rhinos are the lineages leading to the living black and white rhinos (*Diceros bicornis* and *Ceratotherium simum*, respectively). These species are characterized by the absence of incisors and the presence of two well developed horns and massive nasals; a »cauliflower-structure« marks the position of the horns. The south Asian rhinos include the Indian, Javan and Sumatran rhinoceroses (*Rhinoceros unicornis*, *R. sondaicus*, and

Dicerorhinus sumatrensis, respectively) and their ancestors. These species have large second lower incisors, which are kept sharp by wear against small upper incisors. The incisors are used in fighting, while the horns (one in *Rhinoceros*, two in *Dicerorhinus*) are small and less important in fighting. The nasals are relatively gracile. The third group consists of various species of *Coelodonta* and *Stephanorhinus* and went extinct during the Late Pleistocene. Like the African rhinos, they lacked incisors and had two well developed horns, but differed from those in having elongate nasals supported by an ossified nasal septum. The position of the horns is again indicated by »cauliflower-structure« on the nasals. The horns are made of keratin (the same material as nails and hair), which usually does not fossilize, but fossil horns of *Coelodonta* are known and are very long. There is a further rhinoceros in the Pleistocene of northern Eurasia, called *Elasmotherium*, which is more distantly related to the three major groups of rhinos. It is a very large form with a huge dome in the middle of the skull, which is commonly assumed to have supported a huge horn. It lived in Asia and Eastern Europe, though there are some problematic records in Western Europe, possibly of Middle Pleistocene age (Guérin 1980; Cerdeño 1998).

2
Left view of the skulls of the rhinoceroses from Neumark-Nord: a) no. 198 – *Stephanorhinus kirchbergensis*; b) HK88:14'3 – *Stephanorhinus hemitoechus*; c) 1996, 47 – *Coelodonta antiquitatis*.
Linke Ansicht der Nashornschädel von Neumark-Nord: a) Nr. 198 – *Stephanorhinus kirchbergensis*; b) HK88:14'3 – *Stephanorhinus hemitoechus*; c) 1996, 47 – *Coelodonta antiquitatis*.

THE RHINOCEROSES OF THE PLEISTOCENE OF EUROPE

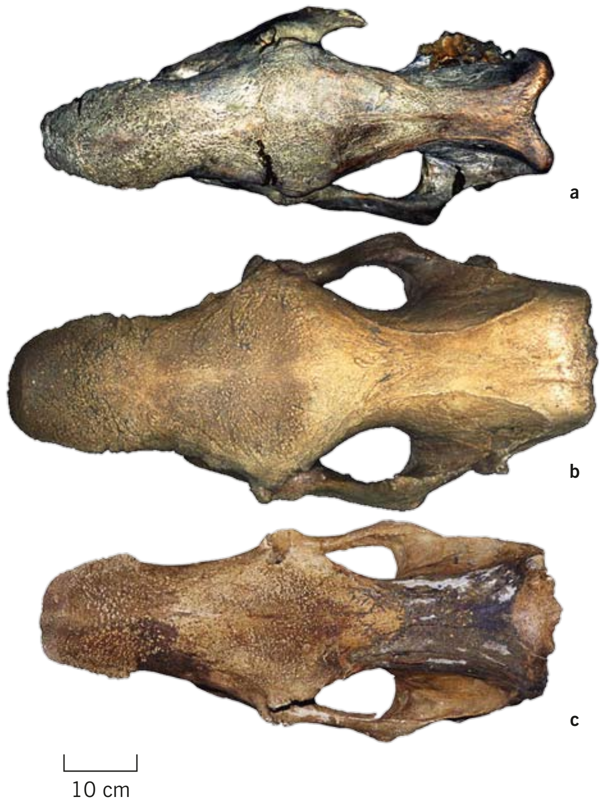
The European species of Pleistocene rhinoceros belong to the third group. Figure 1 gives their distribution in time. The European Pleistocene rhinoceroses are dealt with by J. van der Made (2000; 2010), F. Lacombat (2006), M. Fortelius et al. (1993) and C. Guérin (1980).

The species *Stephanorhinus etruscus* made its appearance in Europe some 3,1–3,2 Ma ago during the Late Pliocene. Its name reflects the fact that it was first recognized from localities in the Arno valley (Italy), where the Etruscans lived. At the beginning of the Pleistocene it was the only species of rhinoceros in Europe.

Some believe *Stephanorhinus etruscus* to have evolved into or to be replaced by *Stephanorhinus hundsheimensis*, a species that was first recognized in Hundsheim (Austria) (Guérin 1980, but using different nomenclature). However, this species has large second premolars, a primitive character, which precludes it from being a descendant of the more advanced *S. etruscus*. In fact, the temporal ranges of both species overlap.

During the Elsterian glaciation (here assumed to have occurred around 650 thousand years ago), the woolly rhino (*Coelodonta*) appeared in Europe. The scientific name refers to a structure in the upper teeth. This genus is known already from the Late Pliocene of northern China and is typical of open or dry landscapes. During glacial periods such landscapes spread into Europe and so did the woolly rhino. Initially it reached Germany, later it appeared in France and during the Late Pleistocene it spread as far as central Spain. While the earliest forms had gracile limb bones, later these became more massive, which might be related to an increase in body weight. Usually all European *Coelodonta* were placed in the species *C. antiquitatis*. The name suggests it is an »old« species, but in fact, it is the youngest one. Recently it was proposed that the oldest European *Coelodonta* be placed in the species *C. tologoiensis* (named after the locality Tologoi, near the Lake Baikal) (Kahlke/Lacombat, 2008).

Stephanorhinus kirchbergensis (first described on the basis of material from Kirchberg in Germany) is a very large species, but not as large as *Elasmotherium*. It appears in interglacial faunas of Europe. Initially it reached Eastern Europe, where it occurred along with the primitive rodent *Mimomys*. After that rodent was replaced by *Arvicola* (another water vole), *S. kirchbergensis* reached Germany and maybe still later France, but it did not reach Spain. Its absence in Europe during glacial periods, notably also in a possible refugia like the Iberian Peninsula (Cerdeño 1990; Van der Made/



3
Dorsal view of the skulls of the rhinoceroses from Neumark-Nord: a) no. 198 – *Stephanorhinus kirchbergensis*; b) HK88:14'3 – *Stephanorhinus hemitoechus*; c) 1996, 47 – *Coelodonta antiquitatis*.
Dorsalansicht der Nashornschädel von Neumark-Nord: a) Nr. 198 – *Stephanorhinus kirchbergensis*; b) HK88:14'3 – *Stephanorhinus hemitoechus*; c) 1996, 47 – *Coelodonta antiquitatis*.

Montoya 2008), suggests that it dispersed each interglacial from Asia to Europe. It is close to *S. choukoutienensis*, from Zhoukoudian near Beijing, and it has been suggested that these are but a single species.

Around 450,000 years ago, *Stephanorhinus hemitoechus* appeared in Europe. The origin of the species is not documented, but it has been suggested that outside Europe it evolved from *S. etruscus* and then dispersed into Europe (Guérin 1980). Whereas *S. kirchbergensis* and *Coelodonta* did not reach Spain, or reached it very late, *S. hemitoechus* is the dominant rhinoceros there, while it is always more rare when it co-occurs with *S. kirchbergensis*. Like *Coelodonta*, *S. hemitoechus* became more robust.

THE RHINOCEROSES OF NEUMARK-NORD

While during the Miocene several species of rhinoceros were often present in a single locality, during the Pleistocene, there is usually one species, or occasionally two, *S. kirchbergensis* and or *S. hemitoechus* or *S. hundsheimensis* together. At Neumark-Nord, there is in addition to these two species also a third one, *Coelodonta*. This is peculiar in that the third species in Europe tends to be restricted to glacial periods. Also in the localities Ehringsdorf (near Weimar) and La Fage (France) these three species are present. All these localities are of the same age. Possibly landscapes were more open or more varied during this interglacial. The three different species are well recognised on the basis of skull morphology (Fig. 2–4).

Coelodonta is represented in Neumark-Nord by a complete skull, the posterior half of a skull and some more minor remains. Typical traits are the massive ossified nasal septum (seen well in lateral view), the extensive cauliflower structure on the nasals and frontals marking the origin of very large horns, a wide and elevated occiput, that overhangs the occipital condyles, and some structure (called medifosette) in the upper molars.

Stephanorhinus hemitoechus is represented by most of a skeleton, including the skull and mandibles, as well as fragments of a second and third skull and several isolated bones and teeth. The skull morphology shows similarities to that of *Coelodonta*: a wide and high overhanging occiput and extensive cauliflower structure marking the origin of two large horns. There are also similarities to *S. kirchbergensis*: the more moderate development of the ossified nasal septum and the morphology of the dentition. A peculiarity in the complete skull is that, behind the third molars, there is on each side a fourth molar, which was in the process of erupting when the individual died. Normally placental mammals have a maximum of three molars in each jaw, while marsupials (like kangaroos) have four. Obviously rhinos are placentals, so this must be an abnormality.

Stephanorhinus kirchbergensis is represented by a nearly complete skull, large part of a second skull, fragments of a third skull as well as isolated bones and teeth. The occiput is narrow and has a V-shape, if seen from above; it does not over hang the occipital condyles and is not much elevated. The nasals are relatively narrow and the area of cauliflower structure is therefore less extensive than in the other species, suggesting a smaller anterior horn. Only the anterior part of the nasal septum is ossified. The upper molars lack a medifosette. A curiosity is that, although *Stephanorhinus kirchbergensis* is much larger than the other Pleistocene European species of that genus and *Coelodonta*, its skull is of the same size, while the sizes of its dentition and body seem to maintain the proportions. As a result, this species has a tooth row that is much larger in comparison to the skull than in the other species. This can be seen well in side view; the tooth row extends from far forward to below the posterior part of the orbit.

RHINOCEROS ADAPTATIONS TO FEEDING

The main herbivores in Old World ecosystems of the past 50 millions of years either are proboscideans, perissodactyls (odd-toed ungulates) or artiodactyls (even-toed ungulates). The odd-toed ungulates, including the rhinoceroses, and the proboscideans are hind gut fermenters, whereas most even-toed ungulates, including camels and ruminants, are foregut fermenters (Janis 2008). There are many differences in the system of digestion of both groups, but some of these are of particular interest here. As their name suggests ruminants ruminate, which means that they chew their food twice and that this makes their digestion more efficient. That is, up to a body weight of 600–1200 kg. In larger animals, the digestive tract is longer and the passage of food through it takes more time. This means that intestinal bacteria have more time to make nutrients available for their hosts. This is why ruminants are seldom very large and why odd-toed ungulates became large when ruminants evolved and diversified. The living species of rhinoceros have adult weights ranging between a little less than one tonne to just over two tonnes. *Coelodonta* and the species of *Stephanorhinus* from Europe may have had body weights between one and a half and three tonnes.

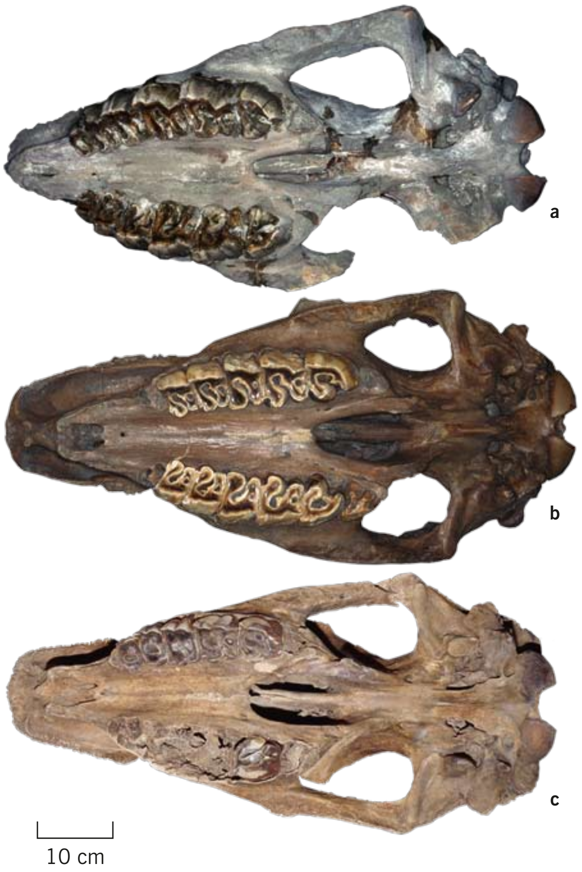
Another difference between the two digestive systems is that if food is very poor, hind gut fermenters can eat more, the passage of food through the digestive tract is more rapid and intake of nutrients increases, though digestion becomes less efficient. This is not possible for ruminants. Small herbivores have higher metabolic rates (because of their small size), and therefore tend to be browsers, which select the most nutritious food, while large herbivores tend to be bulk-feeders, which eat unselectively large quantities of poor food, often grass. Of course these feeding strategies are not separate, but grade into each other, with the so-called mixed feeders in between.

In general, browsers tend to be territorial in closed environments, larger herbivores tend to be territorial during part of the year, and large grazers tend to live in large herds that migrate and thus select for the growth stage of grass.

After these generalities, one might expect rhinos to be grazers, but surprisingly, four of the five living species of rhinoceros are browsers, while only the white rhino is a real grazer. This species has cheek teeth with high crowns to compensate for wear caused by phytoliths in the grass and by occasional intake of sand grains along with the grass. The browsing species of rhinos have cheek teeth with much lower crowns. In general, grazers tend to have cheek teeth with more complex occlusal patterns, often with thinner enamel (at least in certain parts of the occlusal surface) and cementum between the cusps or crests of the teeth.

Also surprisingly, the grazing white rhinoceros is territorial (Estes 1991). Territorial fights between males are not common, but when they occur may result in broken ribs. One of the ribs of the *Stephanorhinus hemitoechus* skeleton from Neumark-Nord was broken and healed. This could reflect a fight between males, but fights between males also occur in non-territorial males because of the dominance order.

How to interpret the diet of the extinct rhinoceroses? The species of *Stephanorhinus* tend to have very low to a little more high crowned molars, in the order: *S. hundsheimensis*, *S. etruscus*, *S. kirchbergensis*, *S. hemitoechus*. The latter species has also more cementum. In the same order the size of the second premolar decreases, which also suggests a more grazing habit. All these characters are a little more developed in *Coelodonta*, which also has an occlusal pattern similar to that of *Ceratotherium*. *Elasmotherium*, which was rare



4
Lower view of the skulls of the rhinoceroses from Neumark-Nord: a) no. 198 – *Stephanorhinus kirchbergensis*; b) HK88: 14'3 – *Stephanorhinus hemitoechus*; c) 1996, 47 – *Coelodonta antiquitatis*.
Untere Ansicht der Nashornschädel von Neumark-Nord: a) Nr. 198 – *Stephanorhinus kirchbergensis*; b) HK88:14'3 – *Stephanorhinus hemitoechus*; c) 1996, 47 – *Coelodonta antiquitatis*.

5
Orientation of the skulls of different rhinoceroses with respect to the vertical (line passing through occipital condyles and occiput) according to Zeuner (1934; figs. 9–11): a) *Rhinoceros sondaicus* (NNML, cat d); b) recent *Diceros bicornis* (NNML, cat a); c) recent *Ceratotherium simum* (NNML, cat b); d) *S. etruscus* from Senèze (Naturhistorisches Museum Basel); e–f) *Stephanorhinus kirchbergensis*, *S. hemitoechus* and *Coelodonta antiquitatis* from Neumark-Nord; h) *Elasmotherium sibiricum* (Paleontological Institute, Moscow); i) *S. hundsheimensis* from Mosbach (Naturhistorisches Museum Mainz) (Skulls not to scale).
Position der Schädel von verschiedenen Nashörnern in Bezug zur Vertikalen (die Linie durchzieht den okzipitalen Condylus und das Okziput) nach F. Zeuner (1934, Abb. 9–11): a) *Rhinoceros sondaicus* (NNML, cat d); b) rezentes *Diceros bicornis* (NNML, cat a); c) rezentes *Ceratotherium simum* (NNML, cat b); d) *S. etruscus* von Senèze (Naturhistorisches Museum Basel); e–f) *Stephanorhinus kirchbergensis*, *S. hemitoechus* und *Coelodonta antiquitatis* von Neumark-Nord; h) *Elasmotherium sibiricum* (Paläontologisches Institut, Moskau); i) *S. hundsheimensis* von Mosbach (Naturhistorisches Museum Mainz) (Schädel nicht maßstabsgetreu).

in Europe, has much more high crowned teeth with very complex occlusal patterns.

Zeuner (1934) suggested that the shape of the posterior part of the skull is related to the possible orientation of the skull and that that reflects the height at which a rhinoceros searches for its food. Grazers eat grass, and have skulls which are directed downwards, while browsers in closed environments search for food at a higher level. He illustrated this with a figure in which the skull orientation is derived from the position of the occiput and occipital condyles relative to the vertical. Figure 7 is similar to Zeuner's figure, but the skulls of the rhinoceroses from Neumark-Nord and other species from the Pleistocene of Europe are added. Most *Stephanorhinus* skulls have an orientation like that of *Diceros*, a browser, while the *S. hemitoechus*, *Coelodonta* and *Elasmotherium* skulls have orientations like that of the grazer *Ceratotherium*.

If these interpretations of the morphology are correct, *Stephanorhinus kirchbergensis* was a browser, *S. hemitoechus* was more of a grazer and *Coelodonta* was still more like a grazer. The fossils from Neumark-Nord present a rare opportunity to test these interpretations. It is common that parts of the plants eaten get into the deep depressions (fossas) in the occlusal surface of the molars of herbivores. This often can be seen in the teeth in the skulls of recent animals in zoological collections. In fossils these plant remains are usually not preserved, because they are oxidised. However, at Neumark-Nord there were good conditions for the preservation of plant material, also for the plant remains in the fossas of the cheek teeth. It is very clear that these remains are not just plant remains that are preserved near the teeth. The fossas of the teeth were covered with sediment and below that cover the fossas were filled with plant remains without admixture of clay or sand (Figure 6).

6

Sampling of plant material from the fossas of the upper cheek teeth of *Stephanorhinus kirchbergensis* (no. 198) from Neumark-Nord.

Entnahme von Pflanzenmaterial aus den Fossae der oberen Backenzähne von *Stephanorhinus kirchbergensis* (Nr. 198) aus Neumark-Nord.

FOOD REMAINS FROM THE TEETH OF THE RHINOCEROSES FROM NEUMARK-NORD

The food remains from the teeth consist of approx. 1–3 cm^3 plant material. The material includes small twigs of maximum 1,5–2 cm length, other wood remains of the same size, bits of bark or cork, small leaf parts, thorns, as well as undefined organic remains and small sediment admixtures. A more detailed description is available (Grube 2003). Plant remains were found in the following rhinoceros fossils of Neumark-Nord (Fig. 7):

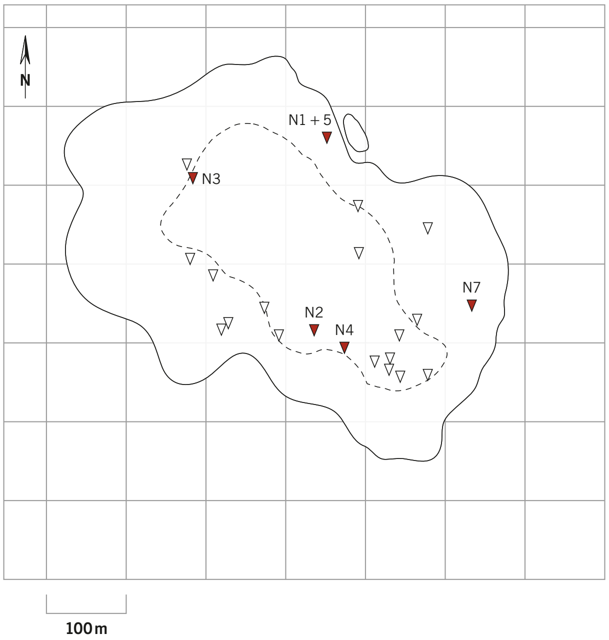
N1 *Stephanorhinus kirchbergensis* (forest rhinoceros): plant remains from the right upper jaw; same individual as N5.

N2 *Stephanorhinus hemitoechus* (steppe rhinoceros): plant remains from skeletal fragments, found in 1987.

N3 *Stephanorhinus kirchbergensis* (forest rhinoceros): plant remains from an upper skull, found in 1987.

N4 *Stephanorhinus kirchbergensis* (forest rhinoceros): plant remains from a find in 1986.

N5 *Stephanorhinus kirchbergensis* (forest rhinoceros): plant remains from the left upper jaw; same individual as N1.



7
Lake basin of Neumark-Nord with the founds of rhinoceroses (continuous line: maximum extent of the lake basin, dashed line: shoreline).
Das Seebecken von Neumark-Nord mit den Funden der Nashörner (durchgezogene Linie: maximale Ausdehnung des Seebeckens, getrichelte Linie: Uferlinie).

N6 *Stephanorhinus kirchbergensis* (forest rhinoceros): plant remains from separated teeth of an individual.

N7 *Coelodonta antiquitatis* (woolly rhinoceros).

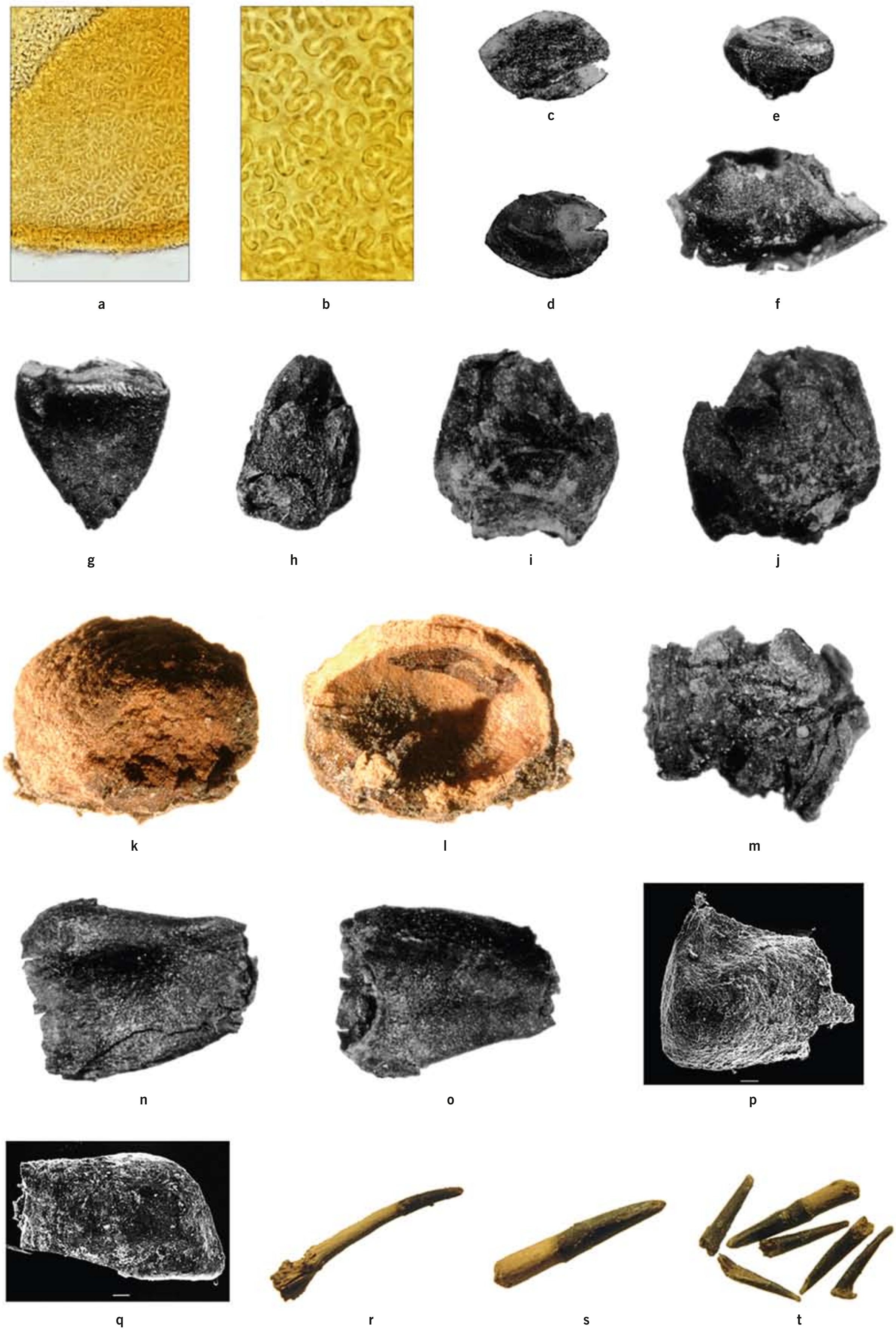
Palynology (spores and pollen): A standardised procedure was used for the processing of spores and pollen (Kaiser/Ashraf 1974; Wissing/Herrig 1999). Unfortunately no evaluable palynomorphs could be found. In particular, the composition of the food remains of the woolly rhinoceros could be an independent indication whether this species really lived during the interglacial or not. This question cannot be answered with the available material and the applied methods.

Cuticles: The anatomy and morphology of the leaf surfaces, in particular the outermost cell layer (epidermis) plays an important role for the diagnostics of plants. The cell walls of the epidermis are usually covered with cutin, a high-polymeric organic macromolecule. The resulting cuticle acts as an additional protective coat, in particular against dehydration. Generally the structures of the epidermis are copied by the cuticle exactly. If the cells are destroyed during the fossilisation, the cuticles remain and show a replica of the cell surfaces (Roselt/Schneider 1969). The preparation of the light microscope samples was done with Schulze's solution. The SEM samples were taken from the elutriated fossil material and were thus free as possible from mineral impurities. After drying they were directly mounted on SEM stubs.

- Cuticle type E: Epidermal cells irregularly isodiametric, in section rectangular to quadratic, sometimes irregularly quadrangular. Distinction between long and short cells not pronounced. Guard cells of the stomata dumbbell-shaped. Due to the construction of the guard cells this cuticle type probably belongs to the grass family Poaceae (»*Graminophyllum*«). The Poaceae have a very typical epidermis pattern. The cells are arranged in oblong rows, whereby in the rows long cells, short cells and, as far as available, the stomata alternates. The short cells are very typical for the grasses, so that they can used like the dumbbell-shaped stomata for the identification of cuticles from this family (Litke 1968; Kac et al. 1977; Westerkamp/Demmelmeyer 1997). Unfortunately the cuticles are very similar within this family, so that a closer identification usually is not possible.
- Cuticle type D (Fig. 8a; 8b): Epidermal cells isodiametric, approx. 60 x 30 µm. Cell walls relatively thick, U-shaped. Because of the undulation the cells seem to be interlocked with one another. No stomata. This is not a cuticle of a leaf epidermis, but rather one of a seed coat (testa). The very specific form of the cells shows similarities with those of the testa from aquatic plants as *Nymphaea* (but not *Nuphar*!) or *Brasenia*. *Brasenia* is not expected in the Intrasaalian interglacial any more. Thus it is possibly from a *Nymphaea*-like plant.

Carpology (fruits and seeds): The material was elutriated and subsequently dried with caution for the separation of the fruits and seeds. Fruits and seeds have a very high diagnostic value. Due to their very specific structure and the presence of various characteristics they can usually be determined very well. Here they are of special interest as food sources for the rhinoceroses. However, unfortunately their number is unusually small so that both the quantity and diversity clearly don't reach those of the buds and the other macro remains. Since this cannot be explained by the preservation conditions or by the processing, the cause has to be sought in the behaviour of the animals themselves. A possible explanation is discussed later.

- *Urtica dioica* L. *fossilis* (Fig. 8c; 8d): Fruit yellowish-grey, matt, nearly elliptical, strongly squeezed, convex on both sides, upward briefly acuminate,



8

Plant remains from the rhinoceroses from Neumark-Nord: a) Cuticle type D (200 x); b) Cuticle type D (500 x); c) Fruit of *Urtica dioica* (20 x); d) Fruit of *Urtica dioica* (20 x); e) Bud type J (20 x); f) Bud scale type D (20 x); g) Bud scale type E (20x); h) Bud type F (20 x); i) Bud type B (20 x); j) Bud type B (20x); k) Endocarp of *Crataegus monogyna* (10 x); l) Endocarp of *Crataegus monogyna* (10x); m) Diaphragm with leaf traces (20x); n) Bud type H (20x); o) Bud type H (20 x); p) Bud scale type K, SEM photo (— = 100 µm); q) Bud scale type G, SEM photo (— = 100 µm); r) Thorn of *Pyracantha coccinea* (3,5 x); s) Thorn of *Pyracantha coccinea* (7 x); t) Thorns of *Pyracantha coccinea* (2,5 x).
Pflanzenreste aus den Nashörnern von Neumark-Nord: a) Kutikula Typ D (200 x); b) Kutikula Typ D (500 x); c) Frucht von *Urtica dioica* (20 x); d) Frucht von *Urtica dioica* (20 x); e) Knospe Typ J (20 x); f) Knospe Typ D (20 x); g) Knospe Typ E (20 x); h) Knospe Typ F (20 x); i) Knospe Typ B (20 x); j) Knospe Typ B (20 x); k) Endokarp von *Crataegus monogyna* (10 x); l) Endokarp von *Crataegus monogyna* (10 x); m) Diaphragma mit Blattabgängen (20 x); n) Knospe Typ H (20 x); o) Knospe Typ H (20 x); p) Knospe Typ K, REM-Foto (— = 100 µm); q) Knospe Typ G, REM-Foto (— = 100 µm); r) Dorn von *Pyracantha coccinea* (3,5 x); s) Dorn von *Pyracantha coccinea* (7 x); t) Dornen von *Pyracantha coccinea* (2,5 x).

downward tapered into a short and thick peduncle; surface slightly verrucous. 1,1 x 0,65 x 0,8 mm (Kac et al. 1965). Found in the forest rhinoceros N5.

- *Crataegus monogyna* Jacq. *fossilis* (Fig. 8k; 8l): Endocarp on both sides slightly tapering, not flattened, always furrowless or only with two weak furrows; Locule elliptical. Found in the forest rhinoceros N5.
- *Prunus spinosa* L. *fossilis*: Small fragment of an endocarp, possibly of *Prunus spinosa*. The exterior view shows the sclerenchyma with a specific rugulate surface structure. Locule with elongated cells in the interior view. Found in the forest rhinoceros N5.

Buds: Buds are short, still compressed shoots whose apex is enveloped by leaves or leaf primordia (often with special bud scales: tegmenta). The identification and evaluation of fossil buds and bud scales is a rather marginal subject in palaeobotany, because of the lower diagnostic value and the ordinarily problematic preservation. In this study the buds unusually appear with the highest abundance (apart from the thorns) and diversity of all plant remains.

- Bud type B (Fig. 8i; 8j): Angiosperm bud with scales, probably Rosaceae (*Pyracantha*??) Found in the forest rhinoceroses N3 and N5.
- Bud scale type D (Fig. 8f): Relatively large. Uncertain botanic affinity. Found in the forest rhinoceros N5.
- Bud scale type E (Fig. 8g): From a bud of the Rosaceae or Betulaceae? Found in the forest rhinoceros N5.
- Bud type F (Fig. 8h): Larger angiosperm bud of rounded cone-shape. Bud scales merlon-like in several whorls around the bud. This bud type is similar to those of *Padus*, *Sorbus* or *Quercus petraea/robur*. Found in the forest rhinoceros N4.
- Bud scale type G (Fig. 8q): Fragment of a bud scale. Uncertain botanic affinity. Found in the forest rhinoceros N5.
- Bud type H (Fig. 8n; 8o): Larger angiosperm bud of rounded cone shape, like type F. At the top a piece was broken off. Bud scales are hardly recognizable. This bud type is similar to those of *Padus*, *Sorbus* or *Quercus petraea/robur*. Found in the forest rhinoceros N4.
- Bud Type J (Fig. 8e): Very small bud. Broader than high, shape like an obtuse-angled cone. Bud scales are hardly recognizable. Uncertain botanic affinity. Found in the forest rhinoceros N5.
- Bud scale type K (Fig. 8p): Fragment of a bud scale of *Populus*. Found in the forest rhinoceros N4.

Other plant remains: During the preparation of fruits and seeds further macro remains were sampled, e. g. small twigs, woody thorns, diaphragms, bark, cork tissue and several wood pieces. Their diagnostic value is generally rather low. The numerous woody thorns in the teeth fossas of the forest rhinoceroses were very conspicuous.

- Thorns of probably *Pyracantha coccinea* Roemer *fossilis* (Fig. 8r–8t): Woody thorns with vascular bundles. Large numbers found in the forest rhinoceroses (in particular N3). The rhinoceroses were surely interested in the juicy fruits or the leaves and unintentionally tore the thorns off the shrub.
- Diaphragm (abscission tissue) of an angiosperm tree or shrub (Fig. 8m): Leaf traces and vascular bundles are partly to be seen. Found in the forest rhinoceros N5.
- Wood, barks of different angiosperm trees or shrubs, cork tissue (partly with bite marks), pieces of twigs, apical tissue, callus tissue etc. were found in the forest rhinoceroses N3, N4, and N5.
- Between the plant remains in the teeth of the forest rhinoceros N3 smaller bone fragments were found, which could not be identified. This would suggest that, this rhinoceros accidentally or intentionally ate vertebrates. As far as we know, such complements to the diet have not been described from living species of rhinoceros.

DISCUSSION AND CONCLUSIONS ON THE DIET OF THE RHINOS

The morphological adaptations suggested that *Stephanorhinus kirchbergensis* was a browser, while steppe rhinoceros *Stephanorhinus hemitoechus* and particularly the woolly rhinoceros *Coelodonta antiquitatis* were more adapted to grazing. Unfortunately we could not recover determinable plant remains from the teeth of the latter species. The plant remains from the teeth of the forest rhinoceros *Stephanorhinus kirchbergensis* belong to *Populus*, *Quercus*, *Crataegus*, *Pyracantha*, *Urtica*, *Nymphaea* as well as plants of the Betulaceae, Rosaceae, and Poaceae. The number of the fruits and seeds unfortunately are very small. A greater diversity was found in cuticles and especially in buds. However, the determinability of these remains is restricted. Particularly, the massive occurrence of thorns has to be emphasized. The following observations on the plant remains in the teeth of *S. kirchbergensis* support the interpretation that it was a browser: 1) the great taxonomic diversity of the plant remains, 2) the abundance of taxa that are no grasses, and 3) the abundance of buds and thorns.

The interglacial of Neumark-Nord has a completely independent floristic character with a strong subcontinental influence, which was brought out by D. H. Mai (1990; 1992) on the basis of carpological investigations. This situation differs clearly from the preceding and the following interglacials. The Flora was dominated by plants, which nowadays occur also in Central Europe, but particularly in Eastern Europe, Western Asia and in the Pontic region. Predominating type of vegetation is the oak steppe forest, which is considerably interspersed by *Acer tataricum* (Aceri tatarici Quercion). This forest formation was broken up by open landscape types such as steppe meadows, steppe heaths and shrubberies. Additionally there was the shore vegetation of the lake. This vegetation is reflected in the food remains of the herbivorous mammals.

There is another hypothesis that could be tested with the results on the diet of the rhinoceroses. T. Pfeiffer (1999) and A. Braun and T. Pfeiffer (2002) studied the the fallow deer *Dama dama* from Neumark-Nord and concluded that the numerous skeletons of deer and other mammals accumulated due to mass deaths caused by intoxication because of cyanobacteria blooms in autumn. The season of death was determined on the basis of osteological criteria of the deer. However, it is not clear how far this statement is valid for other animal species. If the results presented here reflect the actual food spectrum of the rhinoceroses at the lake of Neumark-Nord, the question can be asked whether the food remains permit conclusions on a seasonal determination of the »last meal« and therefore the time of dying (The fact that there was a seasonal regime in the interglacial of Neumark-Nord is supported by varves and tree rings). The ration of seed/fruits to buds plays an important role to solve this problem. From the low abundance of fruits and seeds and the strong occurrence of buds in the food remains it can be concluded that the food intake must have taken place at the beginning of the vegetation period at the end of winter or in the beginning of spring. In this respect this time span also marks the season of dying. Therefore it seems that the rhinoceros individuals, of which we have information, died in another season than the fallow deer and that the deaths of deer and rhinos occured in different events.

ACKNOWLEDGEMENTS

We thank Prof. D. Mania for inviting us to participate in the Neumark-Nord team, Prof. H. Meller for inviting us to participate in the exhibition catalogue, and B. Engesser, H. Lutz, I. Vislobokova and J. de Vos for access to comparative material. JvdM benefitted from support by DFG through Prof. Mania and from the projects CGL2006-13532-C03-03 and CGL2008-03881 of the Spanish Ministerio de Ciencia y Inovación, as well as the Unidades Asociadas Program of the CSIC. RG wishes to thank Prof. D. H. Mai for allowing access to the material and for helpful assistance as well as Dr. U. Bröring and H.-G. Wagner for useful help.

Source of figures

1 after Van der Made 2000; 2010, modified
2–6 J. van der Made, Madrid
7 D. Mania, Jena
8 R. Grube, Berlin

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